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THIS VOLUME IS DEDICATED IN MEMORY OF

ROBERT HAROLD COMPTON (6/8/1886—11/7/1979)

M.A. (Cantab.), D.Sc. (Cape Town), F.R.S.S.Af.

July the 3rd 1979 was an unusually mild winter's day in Cape Town. Taking advantage of the warm sunshine, Prof. Compton lunched at the Kirstenbosch restaurant before proceeding to the herbarium, where he spent part of that afternoon chatting to the staff and casting an approving eye over some newly acquired cabinets. During the past few

years we had become accustomed to these periodic visits. Though nearing his 93rd birthday, 'Cummy', as he was affectionately known, found much satisfaction in lunching at Kirstenbosch, after which he would spend an hour or two in the herbarium, taking his pleasure among the specimens and books he had so painstakingly gathered together. But we had no inkling that this was to be his last visit to Kirstenbosch, for he died suddenly in Cape Town, eight days later, after a brief bout of pneumonia. His passing ended a lifetime of distinguished and devoted service to Kirstenbosch, as well as to the whole cause of botany in South Africa.

He accomplished more than most men can ever hope to fulfil in a lifetime. A scintillating academic career at Cambridge was followed by a year of fundamental botanical exploration in New Caledonia, then (1914) still very much *terra incognita*, botanically speaking. Arriving at Kirstenbosch in 1919 he took over the directorship of a struggling, six year old botanic garden, yet by the time he retired, Kirstenbosch had been built up into an institution of world renown. He established this Journal, editing it single-handed until his retirement. He founded the herbarium which now bears his name, living to see it grow from a single initial sheet, to over a quarter of a million. Retirement saw no diminution of activity. The first twelve years of retirement were spent surveying the vegetation of Swaziland, and then, when in his eighties, he sat down to write up a 684 page *Flora of Swaziland*, enumerating 2 118 species.

Compton's life was one of creating, building, achieving and succeeding in his chosen field. But it was not wholly dominated by botany. Mountain climbing, literature, music (he was an accomplished pianist), were outlets of abiding satisfaction. Indeed, less than a year before his death, he was indulging in the delights of Cape Town's ballet season, despite suffering from slight deafness, the only serious physical affliction to impair his otherwise vigorous physique. His was a tidy life; what he started, he completed. When he died he left no loose ends, no unfinished works. He had run the race and finished the course.

Robert Harold Compton was born at Tewkesbury, Gloucestershire, on the 6th of August 1886, the son of Robert Ernest Compton and his wife Eleanor (born Wilkes). At first, young Robert attended Abbey House School at Tewkesbury. There, at the age of eleven, he had an early, doubtless significant, introduction to botany. It came in the form of a school prize; W. J. Gordon's *'Our Country's Flowers, being a complete guide to the flowers and ferns of Britain'*. After some time he proceeded to Mill Hill School, London, where he completed his

schooling before going up to Cambridge in 1905. Here again, one cannot help noting strong botanical connections, for Mill Hill School occupied a site where the famous Quaker botanist, Peter Collinson, had established his botanic garden and which was later to become the home of another well-known botanist, R. A. Salisbury.

On entering Gonville and Caius College, Cambridge, in 1905, Compton commenced his serious botanical career. There he took the Natural Science Tripos (Part I), obtaining a first class pass in 1907. Two years later, he took Part II of the Natural Science Tripos, again obtaining a first class pass but with distinction in Botany—an achievement which led to the award of a Drosier Fellowship in his college. His earliest papers dealt with anatomy and morphology. Later he was much preoccupied with the genetics of right- and left-handedness in cereals and in 1911, attended the 6th International Genetics Conference in Paris to read a paper on this subject. Self-sterility was another topic which received attention before he returned to anatomy and morphology, this time concentrating on seedling structure. Then, in 1914, the Royal Society and the Percy Sladen Trust Fund, sponsored an expedition to New Caledonia and the Isle of Pines. Compton participated in the year-long expedition which brought him into contact with a flora of wonderful diversity and, not unnaturally, caused him to switch his interests to taxonomy. He made just on 2 500 collections, many of them novelties, including two new gymnosperm-ous genera *Austrotaxus* and *Callitropsis*, which he described himself.

Compton later remarked that his sojourn in New Caledonia was the happiest year of his life. It was certainly to set the pattern for much of what followed. Born at the height of Queen Victoria's Imperial reign, it was only to be expected that he imbibed something of the spirit of that age; an age which encouraged men to go forth to remote lands to initiate developments and to build from the beginning. New Caledonia had taught him how to make pioneering starts, to conquer new frontiers, to lay basic foundations. So it was to be in South Africa. Henceforth he would forsake the rigorous laboratory work and stimulating conviviality of college life at Cambridge, which had been his whole world.

The dual vacancy at Kirstenbosch and the University of Cape Town, resulting from Pearson's death, must have seemed an irresistible challenge. Compton reached out and took it. Arriving with his family in 1919 (he had married Katherine Askin Sealy in Sydney in 1915), he found the fledgling botanic garden at Kirstenbosch had progressed little in the six years since it had been founded. Yet with faith and hope, though precious little charity from the central government,

Compton and Mathews built a botanic garden of global repute. Together they generated a world-wide interest in the cultivation of South African plants. Again, he was breaking new ground. Compton's contributions to horticulture were acknowledged in 1935, when he received the rare distinction of being made an Honorary Fellow of Royal Horticultural Society.

Demands on his time came chiefly from the day to day administration of Kirstenbosch, as well as shouldering a share of the teaching load in the University of Cape Town's Botany Department. Time available for research was lamentably short, yet he pursued his interest in taxonomy with characteristic vigour. He never attempted a generic revision but instead saw systematic botany in a pioneer phase, being content to describe new taxa where necessary. These amounted to 11 new genera and some 212 new species.

Exploring the high Cape Mountains was a regular weekend pre-occupation; gathering seed to stock the garden and herbarium specimens for the Bolus Herbarium, which, since 1924, had been housed at Kirstenbosch, though remaining the property of the University of Cape Town. Collecting in unexplored areas seemed especially to attract him, so, while undertaking periodic visits to the Karoo Garden at Whitehill, Compton commenced a survey of that district's flora. It was a daunting task, undertaken in trying physical conditions, yet this was the sort of work Compton seemed to thrive on. Arriving by train at either Whitehill or Matjiesfontein, he would stride out across the Karoo for an hour or two before reaching the Witteberg and then ascending its slopes to new collecting areas. Between 1921 and 1930 he collected over 700 species of flowering plants and ferns in the Whitehill district, from which area he described four new genera and forty-nine new species!

Like all his earlier South African collections, they were placed in Bolus Herbarium, then housed at Kirstenbosch. All along, he had maintained that no botanic garden could function without the services of an herbarium in its midst. One can therefore understand his great distress when, at Mrs. H. M. L. Bolus' behest, the University of Cape Town decided to move the Bolus Herbarium from Kirstenbosch to the new Groote Schuur campus, a move which was completed in 1938. The removal of the Bolus Herbarium was undoubtedly the greatest setback Compton ever suffered. Yet with quiet determination he set out to establish a new garden's herbarium. Once again he had to make a fresh start. Lesser men may not have had the physical or moral strength to start a new herbarium: fortunately, Compton did.

In 1937 he reported:—"The purchase of cabinets made it possible . . .

to arrange various collections as the nucleus of a Gardens Herbarium''. It was probably the boldest, most important step he ever took as Director of the National Botanic Gardens of South Africa. Working weekdays and weekends, the herbarium was built up sheet by sheet until it had become a workable entity. His own collection of books formed the nucleus of the herbarium library and on his death the remainder of his library was bequeathed to the Compton Herbarium.

The founding of the *Journal of South African Botany* in 1935 was another courageous initiative. There had been no satisfactory local medium, open to all contributors, for the publication of research on the South African flora until this journal made its appearance. Unaided, he edited it until his retirement, making contributions to many issues himself.

When he retired in 1953, Prof. and Mrs. Compton settled in Swaziland on their farm Ukutula near Mbabane. Yet again he was to begin another ambitious project, *de novo*. His interest in the vegetation of Swaziland had been aroused in 1947, when he first visited that country. Soon after settling there, the Swaziland Government asked him to initiate a botanical survey of the Protectorate and in 1955 the survey got under way, supported by the British Colonial Development and Welfare Fund. Unfortunately, the withdrawal of financial support in 1966 forced Compton to discontinue his field work in March of that year, although by this time he had already made over 11,000 collections in Swaziland. This material was largely identified at the Botanical Research Institute, Pretoria, where the first set is now deposited.

Shortly after the publication of his preliminary results in 1966, as *An annotated check list of the Flora of Swaziland*, he began work on the text of a full-scale *Flora of Swaziland*, with keys and descriptions. In 1971 Prof. Compton returned to Cape Town, where he lived with his daughter and son-in-law. It was a move which enabled him to make regular visits to the herbarium at Kirstenbosch and thus make real headway on the manuscript of his flora. He was then 85 years of age! Compton's *Flora of Swaziland* was published on the 6th of August 1976, his 90th birthday.

These are but the bare facts of a man's life as a successful scientist and administrator. Above all, he was a most warm-hearted, genial person, an urbane gentleman whose quiet dignity belied a charismatic charm. His respect for nature and all forms of life was paramount. All that was brash, crude or vulgar, repelled him. Intemperate language had no place in his vocabulary. Though very much a man of this century who lived life to the very end with resounding zest, his calm gentle manner recalled a softer more leisurely age. The whole tempo and spirit of his

life is marvellously illuminated in four charming articles written when in his nineties (*Veld & Flora* vols 62 and 63). Here he tells his own story better than anyone else could.

Many honours came to him. He was president of the Mountain Club of South Africa from 1940 to 1953 and was made an honorary life member in 1963. The South African Association for the Advancement of Science awarded him the South African Medal, the Royal Horticultural Society honoured him with the Veitch Gold Medal and the University of Cape Town, where he had occupied the Harold Pearson Chair of Botany for 34 years, conferred on him the degree of Doctor of Science, *Honoris causa* in August 1968.

Comptonella Bak. fil. a New Caledonian genus of the Rutaceae and the South African *Comptonanthus* B. Nordenstam (Asteraceae) are genera commemorating his name, as do the specific epithets of at least a dozen New Caledonian and over twenty South African plants, including *Protea comptonii* and *Erica comptonii*.

On retiring in December 1953, a fine portrait in oils by Captain Douglas Wales-Smith, was hung in the herbarium, where he had spent so much of his time—the collection thereafter being designated the Compton Herbarium, by resolution of the Board of Trustees.

Together, the Compton Herbarium and this Journal, remain his most enduring memorials.

J. P. ROURKE

COLLECTING DATA

1. *New Caledonian collections*
   Numbers 1–2500 at the British Museum (Natural History). Field Note books and collecting registers of this period are presently in the Compton Herbarium Kirstenbosch but will shortly be presented to the British Museum (Natural History).
2. *Southern African Collections*
   Numbers 2501–32550 at BOL, NBG and K. (The Swaziland Survey commences at about 23,800, with the First set at PRE, Second set at NBG and Third set at K). Registers of this period at NBG.

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1979. Rights and Lefts. *Veld & Flora* **65** (4): 128–129.

Jl S. Afr. Bot. 46 (1): 1–5 (1980)

THE IDENTITY OF *ANTIZOMA HARVEYANA* MIERS EX HARV. AND *A. CAPENSIS* (L.f.) DIELS

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Abstract

An examination and evaluation of available evidence leads to the conclusion that *Antizoma harveyana* Miers ex Harv. must be regarded as a synonym of *A. angustifolia* (Burch.) Miers ex Harv.; that *Antizoma capensis* L.f. Diels must be returned to *Cissampelos* and that the variety *Antizoma capensis* L.f. Diels var. *pulverulenta* (Harv.) Diels must be reduced to synonymy under *Cissampelos capensis* L.f.. Consequently, the number of *Antizoma* species is now reduced to two.

Uittreksel

DIE IDENTITEIT VAN *ANTIZOMA HARVEYANA* MIERS EX HARV. EN *A. CAPENSIS* (L.f.) DIELS

'n Ondersoek en evaluasie van beskikbare getuienis lei tot die gevolgtrekking dat *Antizoma harveyana* Miers ex Harv. as 'n sinoniem van *A. angustifolia* (Burch.) Miers ex Harv. beskou moet word; dat *Antizoma capensis* L.f. Diels oorgeplaas moet word na *Cissampelos* en dat die variëteit *Antizoma capensis* L.f. Diels var. *pulverulenta* (Harv.) Diels as 'n sinoniem van *Cissampelos capensis* L.f. beskou moet word. Gevolglik word die getal *Antizoma*-spesies nou tot twee verminder.

1. Antizoma harveyana

Miers (1851) created the genus *Antizoma*, based on material collected in various parts of Southern Africa. Eight years later, Harvey (1859), published the names of five species belonging to this genus.

The following three taxa, already known at that time, were transferred from *Cissampelos*.

Antizoma angustifolia = *Cissampelos angustifolius* Burch. (1822) *non*. E. Mey. (1847).
Antizoma calcarifera = *Cissampelos calcarifera* Burch. (1824).
Antizoma miersiana = *Cissampelos angustifolia* E. Mey. (1847), *non* Burch. (1822).

The other two newly published species were: *Antizoma harveyana* Miers ex Harv. and *A. burchelliana* Miers ex Harv.

Durand et Schinz (1898), rejected the genus *Antizoma* and simultaneously changed the rank of *A. harveyana* and transferred it to *Cissampelos* as a subspecies of *C. angustifolius* Burch.

Accepted for publication 17th October, 1978.

Diels (1910), however, accepted the genus *Antizoma* and retained the species *A. harveyana* and *A. miersiana*, but erroneously regarded *A. angustifolia* and *A. burchelliana* as synonyms for *A. calcarifera*.

At present, due to the priority of the basionym, the combination *Antizoma angustifolia* (Burch.) Miers ex Harv. is regarded as valid with *A. burchelliana* and *A. calcarifera* as synonyms.

Thus, up to now, *A. angustifolia, A. capensis* [transferred from *Cissampelos* by Diels (1910)] *A. miersiana* and *A. harveyana* have been regarded as distinct species.

According to Diels (1910, p. 307):

"Branches pubescent; Sepals on the outside pubescent; the synandrium 8–locular ..... *A. angustifolia* *(= A. calcarifera)*

Branches glabrous; the sepals on the outside minutely pilose or glabrous; the leaves presently becoming glabrous; synandrium 4–6–locular .. A. harveyana."

the only characteristics by which *A. angustifolia* and *A. harveyana* can be distinguished from one another, are the difference in indumentum of the different parts of the two plants and the number of locules of the synandrium.

The number of locules of the synandrium, however, cannot be regarded as a distinguishing characteristic, because it varies from 4–14 in both taxa, with no definite number of locules even in flowers of the same plant.

When taking other aspects, such as external morphology of the vegetative and reproductive parts (excluding the indumentum), anatomy, fruit and pollen morphology into consideration, there is virtually no difference between *A. angustifolia* and *A. harveyana*.

Regarding the indumentum, a survey of the two taxa showed that *A. harveyana* is never wholly glabrous and that intermediates exist between the two species.

Furthermore, keeping in mind that certain species, e.g. *A. angustifolia* and *A. capensis*, usually have a better developed indumentum in regions such as South West Africa (experiments in hot houses with *Cissampelos torulosa* and *C. hirta* confirm this), the separation of *Antizoma harveyana* and *A. angustifolia* in two taxa, becomes dubious. The two taxa are therefore combined.

Antizoma angustifolia (Burch.) Miers ex Harv. in Harv. et Sond., F.C. **1:** 13 (1859); Miers in Contrib. Bot. **3:** 200 (1871); Diels in Engl., Pflanzenr. **IV**–94:308 (1910); Burtt Davy in Kew Bull.: 341 (1921); Merxm., F.S.W.A. **38:** 2 (1968).

Cissampelos angustifolius Burch., Trav. **1:** 389 (1822) non E. Mey. (1847); Type: Griqualand West, *Burchell 1717* (PRE, iso.!).

Antizoma calcarifera (Burch.) Miers, Ann. Mag. Nat. Hist. ser. 2,**7:** 41 (1851); Miers ex Harv. in Harv. et Sond., F.C. **1:** 12 (1859); Diels in Engl., Pflanzenr. **IV**–94: 308 (1910).

Cissampelos calcarifera Burch., Trav. **2:** 266 (1824). Type: Lower Campbell, *Burchell 1795* (PRE, iso.!).

A. burchelliana Miers ex Harv. in Harv. et Sond., F.C. *loc. cit.* Type: Lower Campbell, *Burchell 1795* (PRE, iso.!).

Antizoma harveyana Miers ex Harv. in Harv. et Sond., F.C. **1:** 12 (1859); Miers in Contrib. Bot. **3:** 200 (1871); Diels in Engl., Pflanzenr. **IV–94**: 309 (1910); Type: Transvaal, *Burke s.n.* (PRE, holo.!). *Cissampelos angustifolius* Burch. var. *harveyana* (Miers ex Harv.) Th. Dur. et Schinz, C. F. Afr. 1.2: 49 (1898).

2. ANTIZOMA CAPENSIS

Linnaeus (f.) (1781) assigned this plant, collected by Thunberg, to the genus *Cissampelos*.

In 1859, Harvey described a variety of this taxon, namely var. *pulverulenta*, which, being pubescent on both sides of the lamina, differs from the typical variety.

Diels (1910) in his survey of the Menispermaceae in Engl. Pflanzenr. IV–94, transferred this species with the two varieties to *Antizoma*.

The reason for this is not very clear, but it was presumably done because the female flower of *Antizoma capensis*, like the other *Antizoma* spp., usually has two sepals and two petals, whereas, according to Diels, the female flower of *Cissampelos* has only one sepal and one petal (rarely two or three petals).

It is evident that he was unaware of the fact that the female flower of *Cissampelos torulosa* usually has two sepals and two petals (in his species description of *C. torulosa* no mention was made of the exact number of sepals and petals).

The morphology of the male flowers of *Antizoma* and *Cissampelos* is very similar. In both genera, the synandrium varies with 4–10 or more locules. In fact, both *Antizoma capensis* and *Cissampelos torulosa* have a 4-loculed synandrium.

Therefore, regarding the morphology of the male and female flowers, *Antizoma capensis* and *Cissampelos torulosa* are very much alike.

Furthermore, when viewing other characteristics of the plants, the similarity between *Antizoma capensis* and *Cissampelos torulosa* becomes more obvious. The outline of the lamina of *Antizoma capensis* shows a greater similarity with that of *Cissampelos*, than with that of the other species of *Antizoma* (Fig. 1).

The leaves of *Antizoma angustifolia* and *A.miersiana* usually have short petioles, varying from 0,5 mm–5 mm, seldom longer, while the longer petiole of *Antizoma capensis* (up to 25 mm) corresponds more closely with that of *Cissampelos* (Fig. 1). The spines or tubercles at the base of the petiole, which are a characteristic feature of both *Antizoma angustifolia* and *A. miersiana*, are absent in *A. capensis* and in *Cissampelos*.

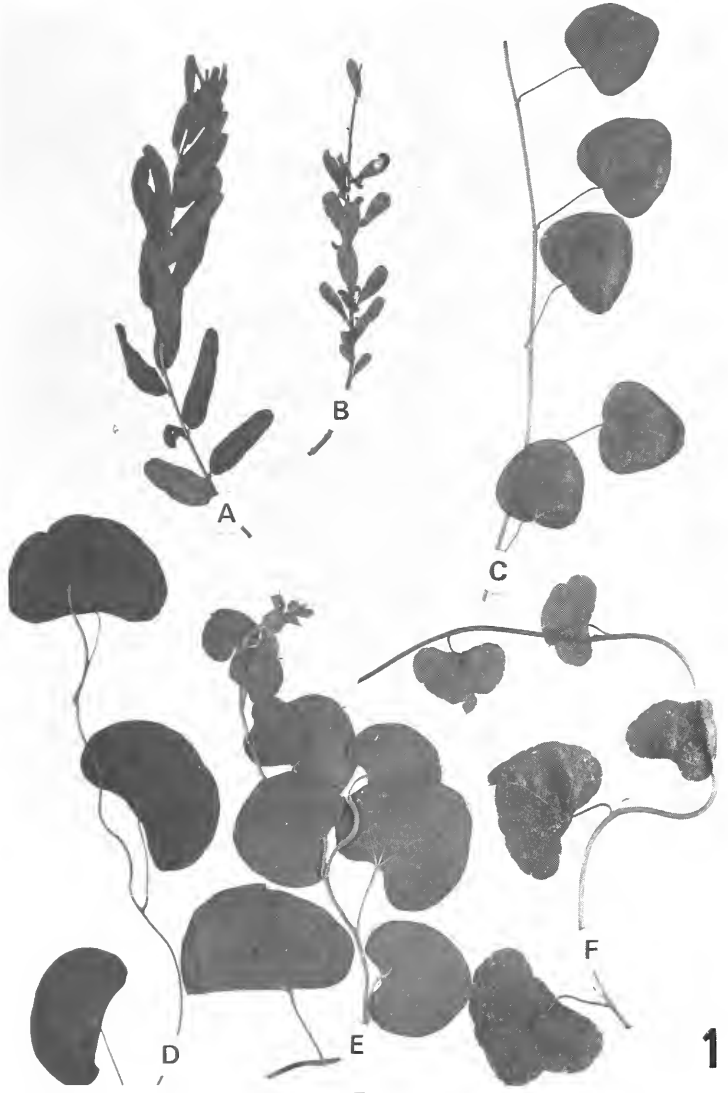

FIG. 1
Vegetative parts, showing the outline of the leaves of *Antizoma angustifolia* (A); *A. miersiana* (B); *Cissampelos capensis* (C); *C. torulosa* (D); *C. mucronata* (E) and *C. hirta* (F).

Contrary to this, the structure of the endocarp of *Antizoma capensis* suggests a closer relationship with the other *Antizoma* spp. while the pollen morphology and anatomy of the leaf and young stem of *Antizoma* and *Cissampelos* are very similar and offer very little help in assigning a specimen to any one of the two genera.

Thus, after studying fresh material as well as all the available herbarium material in South Africa, and taking the above-mentioned facts into consideration, I am convinced that the variety described by Harvey should be reduced to synonymy and the name *Antizoma capensis* must be changed back to *Cissampelos capensis*.

Cissampelos capensis L.f., Suppl.: 432 (1781); Thunb., Prodr.: 110 (1800); DC., Syst. Nat. **1:** 538 (1818); ——— Prodr. **1:** 102 (1824); Harv. in Harv. et Sond., F.C.: 11 (1859); Miers in Contrib. Bot. **3:** 187 (1871). Type: Cape Province; *Thunberg s.n.* Herb. no. *23798* (UPS, syn.; only photo seen).

C. capensis L.f. var. *pulverulenta* Harv. in Harv. et Sond., *loc cit*..

C. humilis Poir. in Lam., Encycl. **5:** 11 (1804). Type: *Sonnerat s.n.* Herb. Lam. (P, syn.; only photo seen).

C. fruticosa L.f., Suppl.: 432 (1781); Ecklon & Zeyher, Enum. **17:** 3 (1834). Type: Cape Province; *Thunberg s.n.* Herb. no. *23800* (UPS, syn.; only photo seen).

Antizoma capensis (L.F.) Diels in Engl., Pflanzenr. **IV**–94: 307 (1910).

A. capensis (L.F.) Diels var. *pulverulenta* (Harv.) Diels in Engl. *loc cit*.; Merxm., F.S.W.A. **38:** 2(1968).

ACKNOWLEDGEMENTS

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AN ANATOMICAL STUDY OF THE STEM AND LEAF OF THE MENISPERMACEAE OF SOUTHERN AFRICA*

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Abstract

The anatomy of the stem, petiole and leaf blade is discussed and illustrated. A tentative key, based on the leaf anatomy, is provided to distinguish between the three different species of *Tinospora*.

Uittreksel

'N ANATOMIESE ONDERSOEK VAN DIE STINGEL EN BLAAR VAN DIE MENISPERMACEAE VAN SUIDELIKE AFRIKA

Die anatomie van die stingel, blaarsteel en blaarskyf word bespreek en geïllustreer. 'n Tentatiewe sleutel, gebaseer op blaaranatomie, word voorsien om tussen die drie *Tinospora*-spesies te onderskei.

Introduction

The name "Menispermum" refers to the horseshoe-shaped fruit and/or seeds found in most of the species. With the exception of a single xerophytic Southern African species, the rest of the members of the family are tropical and subtropical lianes, shrubs or suffrutices.

The family is not very large. Willis (1973), recognises 65 genera with 350 species and varieties. According to Troupin (1962), approximately 25 genera with 101 species are found in Africa. 7 Genera with 13 species and 2 varieties occur in Southern Africa.

The small number of species assigned to a relatively large number of genera is interesting when it is taken into account that the family is probably very old. According to Diels (1910), fossilised wood of this family is known from the Tertiary of Hungary and fossilised leaves from the Cretaceous of Northern America and Greenland. Chesters (1957), records fossilised fruit in deposits from the Miocene of Central Africa.

Various authors contributed to our present knowledge on the anatomy of this family, e.g. Prantl (1891), Maheu (1902), Krafft (1907), Solereder (1908 a, b), Rudolph (1909), Diels (1910), Metcalfe and Chalk (1965) and Van der Walt,

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Schweickerdt and Van der Schijff (1970). The approaches of these authors differ greatly. Some of these studies are very synoptic and contain little information regarding the Southern African species while others pay more attention to anomalous growth.

From the taxonomic point of view, a shortcoming in most of these studies is that very little attempt was made to relate anatomical characteristics to the taxonomy of this taxon. This is especially the case with taxa below the rank of family.

In a discussion of the significance of anatomical features and their value in relation to taxonomy in general, Davis and Heywood (1973), conclude that anatomical features may have a value as diagnostics or in determining relationship, but that endomorphic criteria are not of equal value in all taxa.

Due to the fact that very little anatomical information is available regarding the Southern African species, an anatomical survey was undertaken. This was done firstly to obtain more information and secondly to determine how anatomical characteristics could be used as an additional aid in the taxonomy of these taxa.

The following species and varieties occur in Southern Africa. Those marked with an asterisk are endemic.

Cocculus hirsutus (L.f.) Diels
Tiliacora funifera Miers
**Tinospora fragosa* (Verdoorn) Verdoorn et Troupin
T. tenera Miers
T. caffra (Miers) Troupin
Albertisia delagoensis (N.E.Br.) Forman
Stephania abyssinica (Dill. et Rich.) Walp. var. *abyssinica*
S. abyssinica (Dill. et Rich.) Walp. var. *tomentella* (Oliv.) Diels
Antizoma angustifolia (Burch.) Miers ex Harv.
**A. miersiana* Harv.
**Cissampelos capensis* L.f.
C. mucronata A. Rich.
C. hirta Klotzsch
C. torulosa E. Mey. ex Harv.

Material and Method

The material studied was collected from different localities. At least two specimens of each species were studied, but where some variation was found, additional material from other localities was examined.

The discussion is based mainly on cross-sections through the median part of the stem internode, petiole and lamina. In the case of the leaves, the central part with the midrib was studied.

Fresh material was collected, cut into suitable lengths, fixed in F.A.A. and dehydrated in T.B.A. according to the method of Johansen (1940). It was then

embedded in paraffin wax, cut at 8 μm with a rotary microtome, stained with Safranin and Fast Green and mounted in D.P.X.

Results

The description of the different tissues is given in the same order as seen in cross section from the outside to the inside of the stem and from the adaxial to the abaxial side of the petiole and lamina.

1. **Stem**

The outline in cross-section varies from elliptic to circular (Fig. 1) and is often lobed.

Epidermis

A cuticle is usually present, even in young stems.

The outer tangential cell walls are usually thickened and cutinised, often up to 12 μm thick as in *Cissampelos hirta* (Fig. 2). This feature was also described by Esau (1965), for *Menispermum*.

In *Cissampelos capensis* the outer tangential walls are usually strongly convex, resulting in the formation of papillae.

Anticlinal cell division often occurs in the epidermis where the development of a phellogen is retarded. This was also recorded by Esau (1965), for other members of this family.

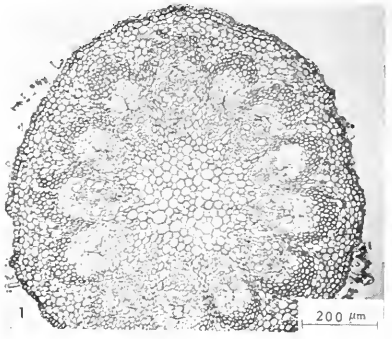


Fig. 1.
Cross-section through the stem of *Cissampelos capensis* illustrating the general internal morphology.

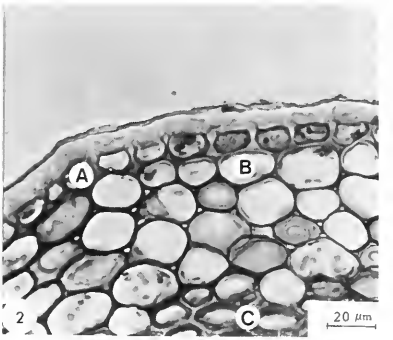


Fig. 2.
Cross-section through the stem of *Cissampelos hirta*. Epidermal cells with cutinised cell walls (A); collenchyma (B) and sclerenchyma (C).

An epidermal phellogen, commonly found in *Albertisia delagoensis* (Fig. 3), was also described for *Tinomiscium petiolare* by Maheu (1902).

Trichomes or hairs usually occur. The most common type is a two-celled uniseriate hair (Fig. 4). Solereder (1908 a, b), Metcalfe and Chalk (1965) and Van der Walt *et al*. (1970), described this same type of hair found in other members of this family.

Multicellular uniseriate hairs as recorded for *Stephania* and *Tinospora* (Metcalfe and Chalk, 1965), were found only in *Stephania abyssinica* var. *tomentella* and not in the three Southern African species of *Tinospora*. None of the above-mentioned authors, however, refer to the multicellular uniseriate weakly-branched hairs (Fig. 5), found exclusively in *Stephania abyssinica* var. *tomentella*.

Stomata of variable size and shape are quite common in the epidermis.

Cortex

This tissue usually occurs as a fairly narrow layer of cells in young stems, e.g. 3–12 cells in *Antizoma angustifolia* or 5–7 cells in *Albertisia delagoensis*. It is clearly differentiated into an outer layer of collenchyma and an inner layer of thin-walled parenchyma cells. Chloroplasts, crystals, tannin and idioblasts (Fig. 6) are often present.

Secretory cells and canals as recorded by Maheu (1906) for *Animirta* are commonly found in *Cissampelos hirta, C. mucronata* (Fig. 7), and *Cocculus hirsutus*.

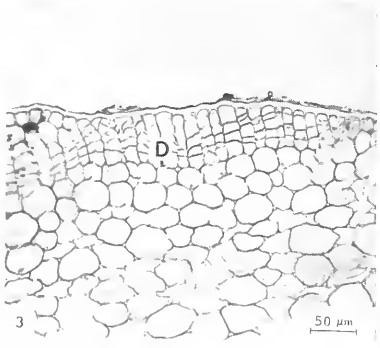
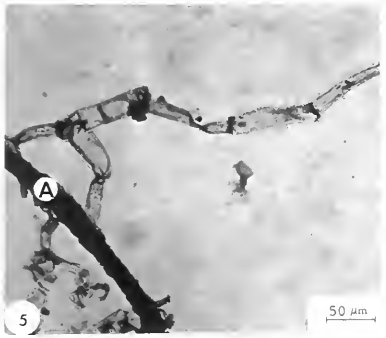
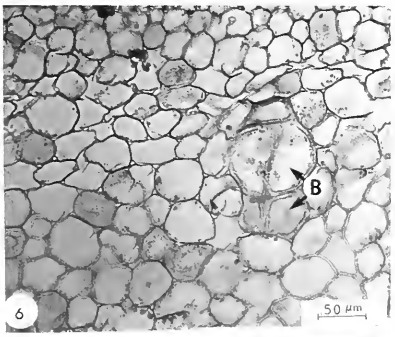
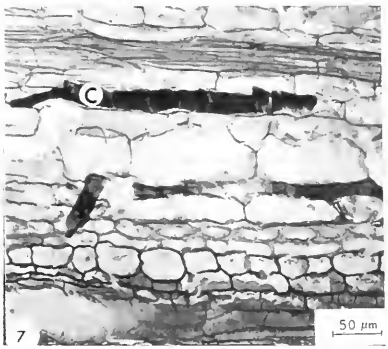


FIG. 3.
Cross-section through the subterranean stem of *Albertisia delagoensis*, showing the epidermal phellogen (D).

FIG. 4.
Two-celled uniseriate hair of *Cissampelos torulosa* as seen in cross-section through the stem.







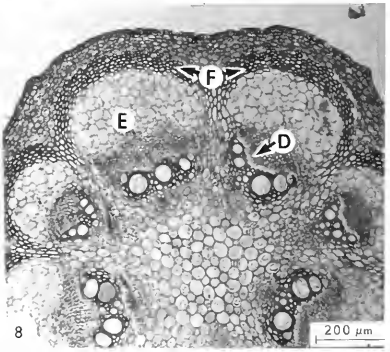


FIG. 5.
Whole mount of multicellular uniseriate branched hairs of *Stephania abyssinica* var. *tomentella*. Part of epidermal cells (A).

FIG. 6.
Cross-section through the subterranean stem of *Albertisia delagoensis*, showing the presence of idioblasts (B) in the cortex.

FIG. 7.
Longitudinal section through the stem of *Cissampelos mucronata*, showing secretory canals with tannin (C).

FIG. 8.
Cross-section through the young stem of *Cissampelos torulosa*. Phloem (D); thin-walled parenchyma tissue (E) and sclerenchyma fibres (F).

The phellogen commonly originates in the cortex of older stems, but in the few exceptions already referred to, may originate in the epidermis.

Pericycle

The term "pericycle" is used here as defined by Metcalfe and Chalk (1965).

In younger stems this tissue is mainly present as a girdle composed of crescent-shaped caps opposite the vascular bundles. It consists mainly of fibres on the outside, and thin-walled parenchymatous tissue to the inside (Fig. 8). In older stems, stone cells usually differentiate opposite the vascular rays between the adjacent caps of fibres (Fig. 9) and the thin-walled parenchyma cells are transformed into fibres (Fig. 24).

Vascular tissue

The bundles are collateral, open and arranged more or less in a circle.

Sieve tubes and companion cells of the phloem are usually easily recognisable and are bordered on the inside by a well-developed vascular cambium. The interfiscicular cambium (Fig. 10) is not always easy perceptible in older stems.

The xylem consists mainly of vessels, fibres and parenchyma cells (Figs 11 and 12). Vessels with exceptionally large diameters (up to 150 μm) were found in the stems of the two varieties of *Stephania abyssinica*.

Pith

This tissue is present in all species and generally well-developed. In the semi-succulent stems of *Tinospora* it may represent more than half of the diameter of the stem.

The central pith cells are usually much larger than the peripheral cells and in *T. caffra*, these central cells may have diameters of up to 12 μm.

Starch grains are usually found in the pith of subterranean stems.

In older stems, the medullary rays are composed of fibres.

2. **Petiole**

The outline in cross-section varies from circular with a flattened adaxial side, to oval, reniform, hexagonal or rhomboidal.

Epidermis

A cuticle, although sometimes very thin, is usually present. The characteristics of the outer tangential cell walls and epidermal hairs are similar to those described for the stem.

Cortex

The ratio of cortex width to petiole diameter is much greater than the ratio of cortex width to stem diameter.

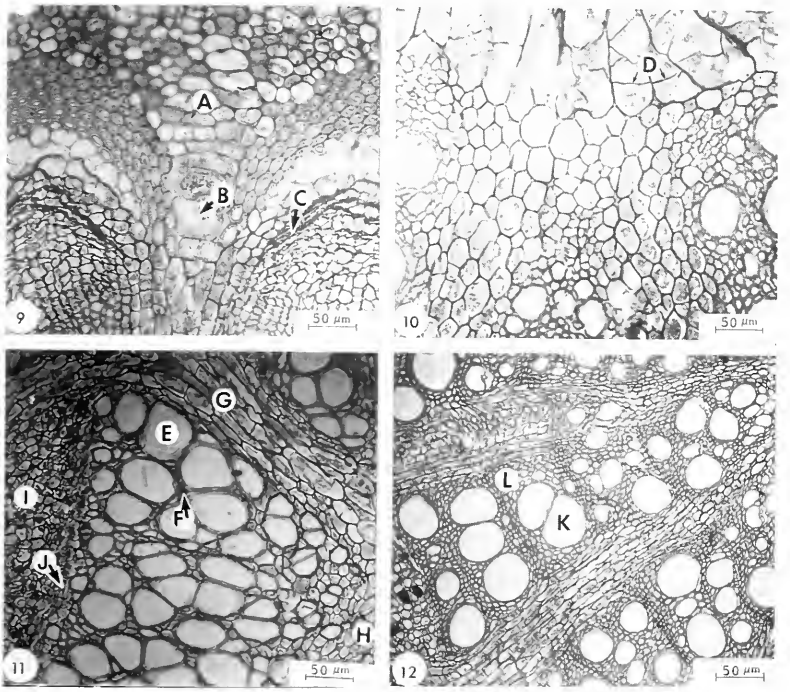


FIG. 9.
Cross-section through the adult stem of *Cissampelos torulosa*. Starch grains (A); stone cells (B) and protophloem (C).

FIG. 10.
Cross-section through the young stem of *Cissampelos torulosa* with interfascicular cambium (D).

FIG. 11.
Cross-section through the vascular bundle of *Stephania abyssinica* var. *abyssinica*. Vessel (E); parenchyma (F); primary vascular rays (G); protoxylem (H); phloem (I) and vascular cambium (J).

FIG. 12.
Cross-section through the secondary xylem of *Cissampelos mucronata*. Vessel (K) and fibres (L).

The cells of the hypodermal collenchyma are usually smaller than the thin-walled parenchyma cells adjacent to the pericycle. The distribution of chloroplasts and tannin is the same as in the stem. No periderm or endodermis were observed in the material examined.

Pericycle

Typical fibre caps, similar to those in the stem, are usually present in *Cocculus hirsutus, Tiliacora funifera, Tinospora* spp., *Albertisia delagoensis* and a few other species. In *Antizoma angustifolia* and *Cissampelos capensis* the pericycle is represented by sclereids only, while it is completely absent in both varieties of *Stephania abyssinica*.

The thin-walled parenchymatous pericycle usually present in the petioli of younger leaves, is absent in the petioli of young leaves of *Antizoma*. In the older petioli of some of the other genera, it is transformed into fibres.

Vascular tissue

The vascular bundles are similar to those in the stem and are arranged either in the form of a V, e.g. *Antizoma angustifolia* (Fig. 13) or in a circle as in *Cissampelos hirta* (Fig. 14) and the majority of the other species. In both cases, the vascular bundles on the abaxial side were found to be of a larger diameter than the rest.

Pith

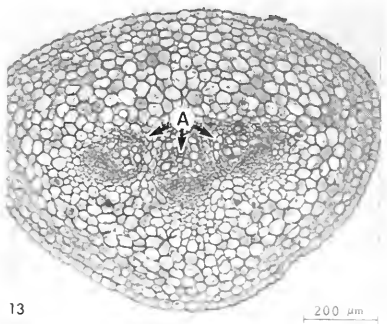
This tissue is mainly recognisable in those species with a circular arrangement of vascular bundles. The medullary rays vary from fairly broad e.g. *Tiliacora funifera, Tinospora* spp., *Stephania abyssinica* (Fig. 15) to narrow, as in *Albertisia delagoensis*.

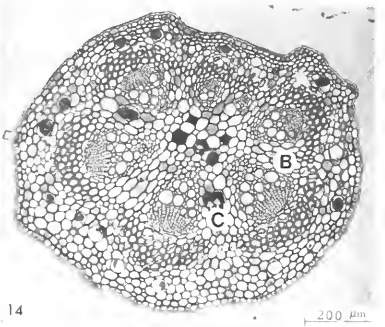
3. **Lamina**

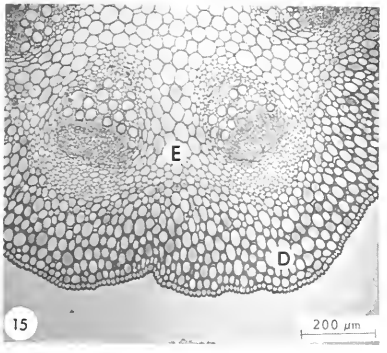
Two types of leaves were found, namely isobilateral and dorsiventral. The leaves of *Antizoma miersiana* (Fig. 16) and the narrower leaves of *A. angustifolia* and *Cocculus hirsutus* are isobilateral, while leaves of *Tiliacora funifera* (Fig. 17) as well as the rest of the members of the family, including the broader leaves of *Antizoma angustifolia* and *Cocculus hirsutus* are typically dorsiventral. No centric leaves as described by Krafft (1907), Solereder (1908 a, b) and Metcalfe and Chalk (1965) for other members of the family, were found.

Epidermis

The cells of the adaxial and abaxial surface of the leaves were found to be of more or less the same size, or those of the adaxial surface were somewhat larger.







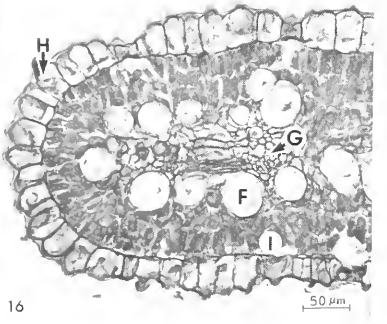


FIG. 13.
Cross-section through the petiole of *Antizoma angustifolia*, showing the outline as well as the vascular bundles (A) arranged in the form of a V.

FIG. 14.
Cross-section through the petiole of *Cissampelos hirta* showing the outline as well as the vascular bundles (B), arranged in a circle. Notice the presence of secretory canals (C) in the petiole.

FIG. 15.
Cross-section through the petiole of *Stephania abyssinica* var. *abyssinica* to show the presence of a well-developed collenchyma (D), the medullary ray (E), and the absence of any sclerenchyma opposite the vascular bundles.

FIG. 16.
Cross-section through the isobilateral leaf of *Antizoma miersiana*. Water tissue (F); Vascular bundle (G); papillose epidermis (H) and palisade parenchyma (I).

The diameter of the epidermal cells of the different species, however, may differ markedly. The largest cells mentioned by Krafft (1908) in a survey of the leaf anatomy of this family, had dimensions of 78 × 58 μm. In this regard the epidermal cells of *Tinospora fragosa* (Fig. 18), with dimensions up to 150 × 150 μm, are exceptional.

The outer periclinal cell walls of the adaxial surface are cutinised and may be up to 8 μm thick as in *Cissampelos hirta*.

Papillose epidermal cells were found in other members of the family by Krafft (1907), Solereder (1908 a, b) and Metcalfe and Chalk (1965). In the Southern African species, this phenomenon is best observed in *Stephania abyssinica* (Fig. 19).

Stomata, usually restricted to the abaxial surface of dorsiventral leaves, are also to be found in the adaxial surface of isobilateral leaves.

No hydathodes as described for *Anamirta* by Krafft (1907), Solereder (1908 a, b) and Metcalfe and Chalk (1965), were found in any of the Southern African species.

Hairs found on both surfaces of the leaves, are similar to those already described for the stem.

An interesting feature in some of the leaves of *Cissampelos torulosa* and *C. hirta*, is the presence of subepidermal mucilage or slime (Fig. 20). As a result of this, the adaxial surface of the leaves exhibits a lead sheen.

Raphides in the epidermal cells of the leaves of *Tinospora fragosa* (Fig. 18) are conspicuous. A survey of other types of crystals of calcium oxalate was given by Solereder (1908 a, b) and Metcalfe and Chalk (1965).

Mesophyll

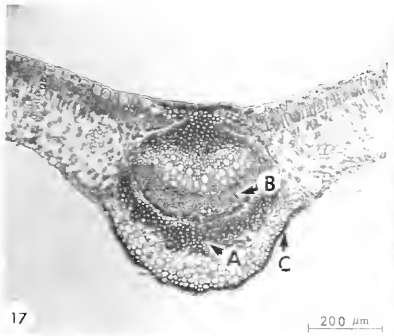
In isobilateral leaves, e.g. those of *Antizoma miersiana* (Fig. 16), this tissue is not clearly differentiated into palisade and spongy mesophyll.

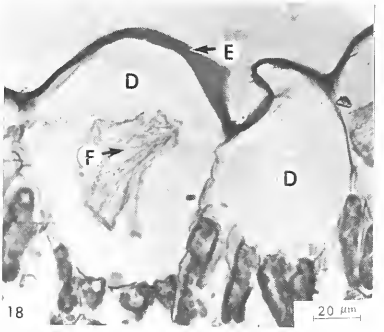
In dorsiventral leaves, the palisade consists of one cell layer only as in *Tinospora* and *Albertisia delagoensis*. In *Cissampelos*, individual cells of a second layer are often visible, while in *Cocculus hirsutus, Tiliacora funifera* and *Stephania abyssinica*, a fully developed second cell layer is often present.

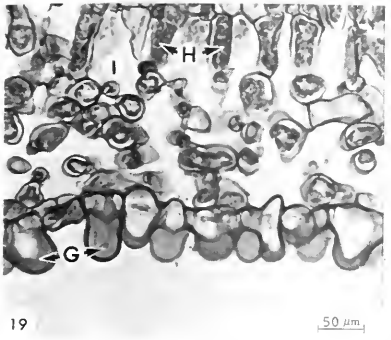
The shape of the cells of the palisade parenchyma may vary from isodiametrical, e.g. *Tinospora fragosa*, to strongly elongated, e.g. five to seven times longer than wide, as in *Tiliacora funifera* and *Tinospora tenera*.

The cells of the spongy mesophyll usually vary in size and shape and are not as closely packed as the cells of the palisade.

In some species, e.g. *Antizoma miersiana*, the parenchymatous or collenchymatous tissue on the adaxial and abaxial sides of the vascular bundles of the midrib is absent so that the mesophyll is continuous (Fig. 21).







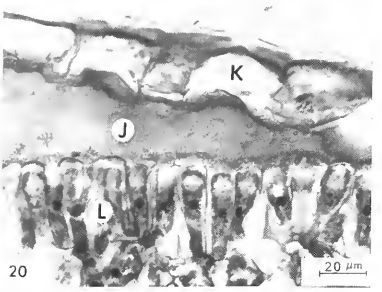


FIG. 17.
Cross-section through the dorsiventral leaf of *Tiliacora funifera*, showing the sheath of sclerenchyma fibres (A), the phloem (B) arranged in the form of a semicircle and the abaxial epidermis (C), usually staining very darkly.

FIG. 18.
Cross-section through the dorsiventral leaf of *Tinospora fragosa* to show the extremely large adaxial epidermal cells (D); the moderately thickened outer cell wall (E) and raphides (F).

FIG. 19.
Cross-section through the dorsiventral leaf of *Stephania abyssinica* var. *abyssinica*. Papillose epidermal cells (G); palisade parenchyma cells (H) and large intercellular spaces (I).

FIG. 20.
Cross-section through the leaf of *Cissampelos hirta* with subepidermal slime (J) between the epidermis (K) and mesophyll (L).

Vascular tissue

Vascular bundles are typically collateral, open and surrounded by a sheath of thin-walled parenchymatous tissue, e.g. *Cissampelos torulosa* (Fig. 22), or sclerenchyma, e.g. *Tiliacora funifera* (Fig. 17). or water tissue, e.g. *Antizoma miersiana* (Fig. 16).

Tannin is commonly found in the cells of the bundle sheath, e.g. *Cissampelos hirta* (Fig. 23).

The hypodermal parenchyma on the adaxial and abaxial sides of the bundle is often replaced by collenchyma, e.g. *C. torulosa* (Fig. 22).

The xylem consists mainly of vessels and parenchyma. A vascular cambium is usually visible in the bundles of older leaves, such as *C. torulosa* (Fig. 22).

Sieve tubes and companion cells of the phloem are not always easy to distinguish. In some species, e.g. in the isobilateral leaves of *Cocculus hirsutus*, or the dorsiventral leaves of *Tiliacora funifera* (Fig. 17), the phloem is arranged in the form of a semi-circle around the xylem.

Discussion

It is significant that, although some adult stems may become semi-succulent, e.g. the different *Tinospora* spp., or woody with diameters up to 180 mm and 220 mm as in *Cocculus hirsutus* and *Tiliacora funifera* respectively, the same basic anatomical structure is found in the younger stems of all species. Even in those that become woody at a very early stage, such as the xerophytic *Antizoma miersiana* this phenomenon is observed. This is quite remarkable when taking the long historical background of this family into account. Adaptation to different environmental conditions thus seems to have little effect on the anatomy of the young stems.

Anatomically the leaves of the different species exhibit greater diversity than the stems. The Southern African species of *Tinospora* can serve as a good example, where anatomical characteristics can be used as an aid to identification where the traditional exomorphological approach of the vegetative parts offers little help in distinguishing between species.

Tentative Key for the Identification of the Different *Tinospora* Species, Based on the Intervein Anatomy of the Leaf

Adaxial epidermal cells of variable size and shape; ratio of anticlinal width of largest of these cells to leaf thickness ±1:2; raphides in epidermal cells common ····· **T. fragosa**

Adaxial epidermal cells of more or less uniform size and shape; ratio of anticlinal width of these cells to leaf thickness ±1:4–1:5; raphides in epidermal cells not very common.

Cells of palisade parenchyma short; ±1–3 times longer than wide.....**T. caffra**

Cells of palisade parenchyma elongated; ±5–7 times longer than wide.....**T. tenera**

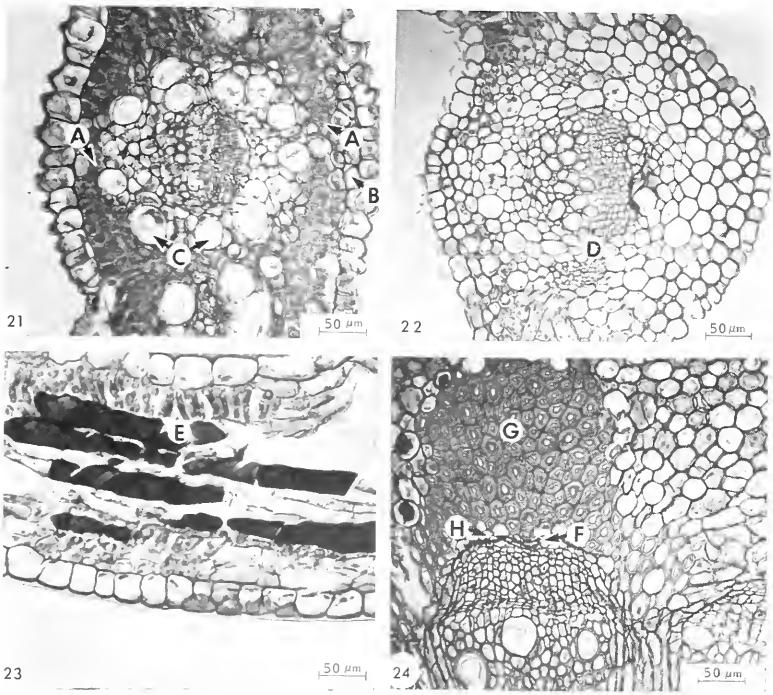


FIG. 21.
Cross-section through the midrib of *Antizoma miersiana* with the continuous mesophyll (A) on the adaxial and abaxial sides of the vascular bundle; collenchyma (B) and water tissue (C).

FIG. 22.
Cross-section through the midrib of *Cissampelos torulosa* to show the vascular cambium (D) and the absence of any fibres in the bundle sheath.

FIG. 23.
Cross-section through the leaf of *Cissampelos hirta* showing longitudinally sectioned tanniniferous bundle sheath cells of a lateral vein.

FIG. 24.
Cross-section through the stem of *Antizoma angustifolia* showing the limited amount of thin-walled parenchyma (H) between the sclerenchyma fibres (G) and protophloem (F).

Conclusion

With the exception of suggesting a possible close relationship between the different members of this family, the anatomy of the stem proved to be of little value in delimiting the different species.

Contrary to this, the anatomical characteristics of the leaf can be used as an aid in solving taxonomical problems in the Southern African Menispermaceae. Such anatomical characteristics are:

(i) The type of epidermal cells.
(ii) The number of layers of palisade parenchyma.
(iii) The absence or presence of tannin in certain cells.
(iv) The characteristics of the sclerenchyma.

Data from these characteristics are incorporated in a numerical taxonomic survey of this group which will be published elsewhere.

Acknowledgements

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THE ENDOCARP OF THE SOUTHERN AFRICAN MENISPERMACEAE

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Abstract

The shape of the fruit and the characteristics of the superficial sculpturing of the endocarp of the 13 species are described and illustrated. The taxonomic significance of these characteristics is pointed out and a key is provided to distinguish between fruit of the different genera as well as between the species of *Tinospora*.

Uittreksel

DIE ENDOKARP VAN DIE SUIDER-AFRIKAANSE MENISPERMACEAE

Die vorm van die endokarp en die aard van die oppervlakpatrone daarop van die 13 spesies word bespreek en geïllustreer. Die taksonomiese belangrikheid van hierdie kenmerke word aangetoon en 'n sleutel word voorsien om tussen die vrugte van die verskillende genusse te onderskei asook tussen die *Tinospora*-spesies.

Introduction

"Menisperma" refers to the peculiar hippocrepiform (horseshoe-shaped) fruit and/or seeds found in the majority of the species of this family.

The plants are dioecious with the flowers mostly inconspicuous. The ovary consists of 1–12 free carpels. The style is very short or absent and the stigma lobed or cleft. Initially, each carpel is erect, containing the ovule with basal placentation, but due to unequal growth during development, it gradually bends inwards to attain its characteristic shape.

The name *Menispermum* was first used by Tournefort, accepted by Linnaeus in his *Species plantarum* (1753) and published by A. L. de Jussieu in his *Genera plantarum* (1789).

The diagnostic shape of the fruit enabled Chesters (1957), to allocate fossilised fruit from the Miocene of Rusinga Island, Lake Victoria, to the extant genera *Cissampelos*, *Stephania* and *Triclisia*.

Miers (1871), Diels (1910) and Troupin (1962) paid some attention to endocarp characteristics. Although illustrations of certain species were provided, the taxonomic importance of the finer detail was not fully realised and exploited. Forman (1956, 1974), however, being aware of the taxonomic value of these endocarp patterns, used them in descriptions and keys of the Malaysian species of *Stephania* and in the description of *Cocculus*.

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Material and Methods

Seven genera, thirteen species and two varieties occur in Southern Africa. Five samples of fruit of each taxon, collected where possible from different localities, were examined.

Fresh and dried fruit were boiled in water, transferred to a 5% cellulase solution in distilled water and left for 12–30 h at 30 °C to dissolve the outer layers of the pericarp. The endocarp was finally cleaned with a stiff nylon brush.

Because of the relatively large size of some fruits, e.g. that of *Albertisia delagoensis* (which may be up to 18 mm in diameter), it was impossible to obtain comparable scanning electron micrographs of all the objects. A Zeiss Tessovar was therefore used to obtain photomacrographs.

Results

The endocarp is bony, with the exception of one genus in which it is parchment-like. The shape is more or less ellipsoidal in a few species and horseshoe-shaped in the remainder of the cases.

The condyle (Fig. 1C), is absent in one genus and in the others varies from linear to narrowly obovate, obovate or forming an enclosed globular cavity within

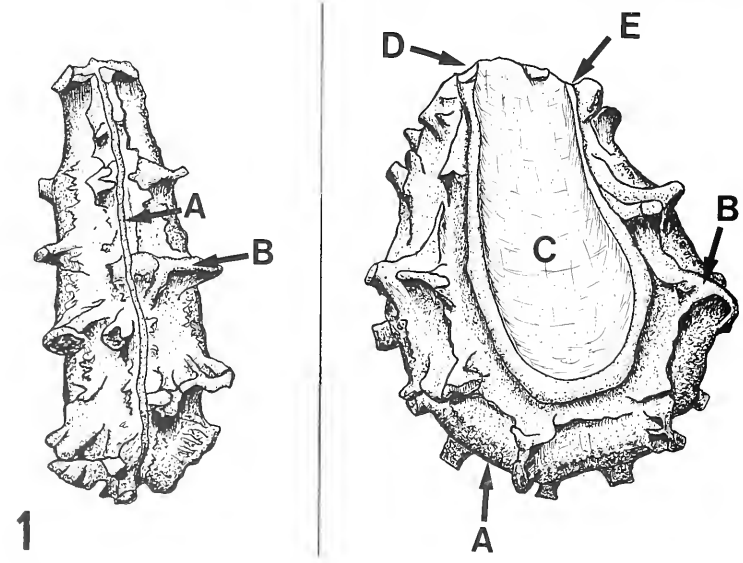

Fig. 1.
Two different views, showing the shape and morphology of the endocarp of *Stephania abyssinica* var. *abyssinica* with dorsal ridge (A); radial ridge (B); condyle (C); position of stigma (D) and attachment of funiculus (E).

the endocarp. Perforation of the septum of the condyle is conspicuous, inconspicuous or absent. The surface of the endocarp is fairly smooth or wrinkled, or exhibits a definite sculpturing in the form of ribs, ridges, knobs or scales.

KEY TO THE GENERA BASED ON THE STRUCTURE OF THE ENDOCARP

Endocarp horseshoe-shaped, condyle linear, narrowly obovate, obovate or more or less circular:
- Condyle more or less circular with the perforation usually conspicuous . . . 1. **Cocculus**
- Condyle linear, narrowly obovate or obovate; perforation very small or absent:
  - Condyle narrow or linear, laterally somewhat convex; surface of endocarp more or less smooth without prominent knobs or tubercles . . . . . 2. **Tiliacora**
  - Condyle narrowly obovate or obovate; laterally somewhat concave; surface of endocarp usually with prominent ridges, knobs, scales or tubercles:
    - Condyle obovate; septum smooth, unperforated; dorsal ridge conspicuous . . . . . 5. **Stephania**
    - Condyle narrowly obovate; septum somewhat rough, often perforated; dorsal ridge inconspicuous or absent:
      - Radial ridges or plates prominent and more or less perpendicular to the surface of the endocarp, or flattened and wrinkled with the lateral girdle, adjacent to the condyle fairly smooth . . . . . 7. **Cissampelos**
      - Radial ridges either flowing into one another, or scale-like and pointing towards the condyle, or sometimes warty; lateral girdles adjacent to condyle fairly rough in texture . . . . . 6. **Antizoma**

Endocarp not horseshoe-shaped; condyle absent or in the form of an enclosed globular cavity within the endocarp:
- Condyle absent; endocarp parchment-like, wrinkled . . . . . 4. **Albertisia**
- Condyle in the form of an enclosed globular cavity within the endocarp; endocarp bony . . . . . 3. **Tinospora**

FIG. 2.
Cocculus hirsutus. Lateral view with perforation (A) conspicuous.

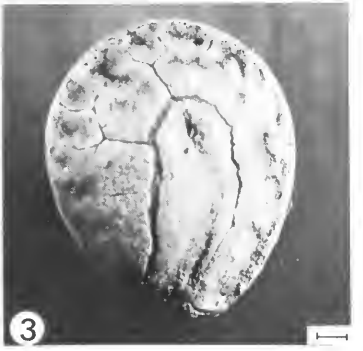

FIG. 3.
Tiliacora funifera. Lateral view.

DESCRIPTION OF THE SPECIES

1. *Cocculus hirsutus* (L.) Diels (Fig. 2)
   Endocarp bony, horseshoe-shaped; condyle more or less circular; septum usually perforated; dorsal ridge sharp, prominent; lateral ridges often inconspicuous and separated from the dorsal ridge by a girdle or irregular ridges; edge of condyle involute, composed of many radial ridges.
2. *Tiliacora funifera* (Miers) Oliv. (Fig. 3)
   Endocarp bony, horseshoe-shaped, laterally somewhat convex, condyle narrow or linear; dorsal ridge inconspicuous with many short radially-arranged shallow grooves; lateral surface with a shallow U-shaped furrow bordering on the condyle.
3. *Tinospora* Miers emend Troupin
   Endocarp bony, ovoidal or more or less ellipsoidal with the condyle as an enclosed globular cavity within the endocarp; surface fairly smooth or with a few distal and proximal knobs.

KEY TO THE SPECIES OF *TINOSPORA*

Condyle elliptic:
  Endocarp ovoidal without any distal or proximal knobs ..... 3.1 **T. fragosa**
  Endocarp more or less ellipsoidal; distal and proximal knobs conspicuous ..... 3.3 **T. caffra**
Condyle with four prominent lobes ..... 3.2 **T. tenera**

3.1 *Tinospora fragosa* (Verdoorn) Verdoorn et Troupin (Figs 4, 5)
Endocarp bony, ovoidal without any distinct knobs or tubercles; condyle elliptic.

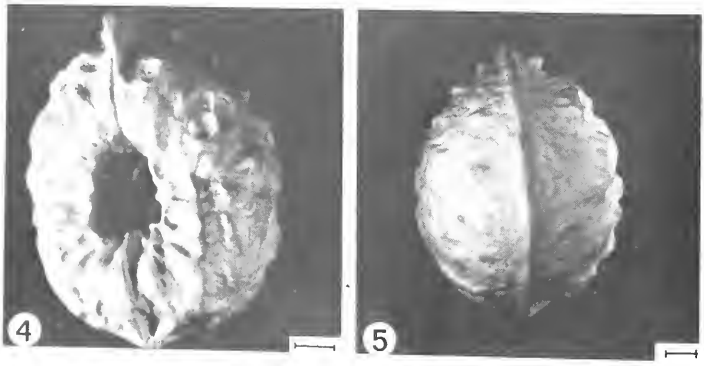

FIG. 4.
Tinospora fragosa. Ventral view.

FIG. 5.
T. fragosa. Dorsal view.

3.2 *Tinospora tenera* Miers (Figs 6, 7)
Endocarp bony, more or less ellipsoidal with base somewhat flattened; distal and proximal knobs conspicuous; condyle with four prominent lobes.

3.3 *Tinospora caffra* (Miers) Troupin (Figs 8, 9)
Endocarp bony, more or less ellipsoidal with base somewhat flattened; distal and proximal knobs conspicuous; outline of condyle elliptic.

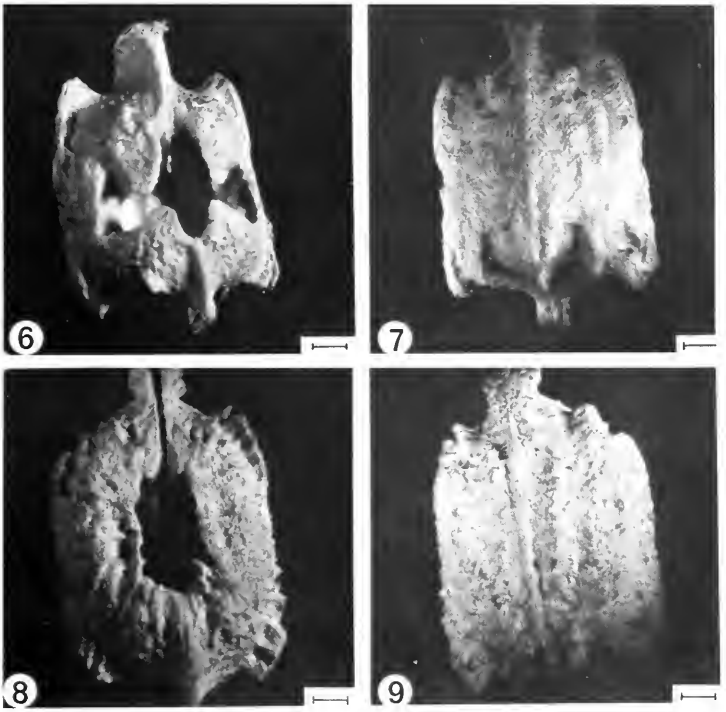

FIG. 6.
T. tenera. Ventral view.

FIG. 7.
T. tenera. Dorsal view.

Each scale division represents one millimetre.

FIG. 8.
Tinospora caffra. Ventral view.

FIG. 9.
T. caffra. Dorsal view.

4. *Albertisia delagoensis* (N.E.Br.) Forman (Fig. 10)
   Endocarp parchment-like, wrinkled without any definite surface sculpturing; not horseshoe-shaped, condyle absent.
5. *Stephania abyssinica* (Dill. et Rich.) Walp. (Fig. 11)
   Endocarp bony; horseshoe-shaped; laterally concave; condyle obovate; septum smooth, imperforate; one dorsal and two lateral ridges very conspicuous and interconnected by radially arranged ridges; the latter sometimes with sharp points.
   The endocarps of the two varieties e.g. *S. abyssinica* (Dill. et Rich.) Walp. var. *abyssinica* and *S. abyssinica* (Dill. et Rich.) Walp. var. *tomentella* (Oliv.) Diels could not be distinguished from one another.
6. *Antizoma* Miers (Figs 12, 13)
   Endocarp bony; horseshoe-shaped; laterally concave; condyle narrowly obovate; septum somewhat rough, often perforated; dorsal ridge absent and replaced by a fissure or shallow furrow bordered on both sides by two or three lateral girdles of radial ridges; radial ridges flattened or sometimes warty radiating from the condyle, lateral girdle adjacent to condyle fairly rough.
   The great similarity in the structure of the endocarps of this genus makes the construction of a key to distinguish between the fruit of the two species, viz. *A. angustifolia* (Burch.) Miers ex Harv. and *A. miersiana* Harv., impossible.
7. *Cissampelos* L. emend Miers (Figs 14, 15, 16, 17)
   Endocarp bony; horseshoe-shaped; laterally concave, condyle narrowly obovate; septum somewhat rough, often perforated; dorsal ridge often inconspicuous or absent and replaced by a fissure or shallow furrow, bordered on both sides by two or three lateral girdles, the latter either composed of radial ridges with prominent plates or tubercles arranged perpendicular to the surface, or with a wrinkled surface, with the lateral girdle, adjacent to the condyle fairly smooth.
   Four species, e.g. *C. capensis* L.f., *C. hirta* Klotzsch, *C. mucronata* A. Rich. and *C. torulosa* E. Mey. ex Harv. occur in Southern Africa, but again, due to the great similarity in the structure of their endocarps, the compilation of a key to distinguish between them has been found impossible.

Conclusions

The features of the endocarp of the Southern African Menispermaceae are so characteristic that they can usually be used as an additional aid to identification.

The similarity in the structure of the endocarp suggests a close relationship between *Antizoma* and *Cissampelos*.

Three endocarp types have been recognised, e.g.:

(i) endocarp ellipsoidal with no condyle;

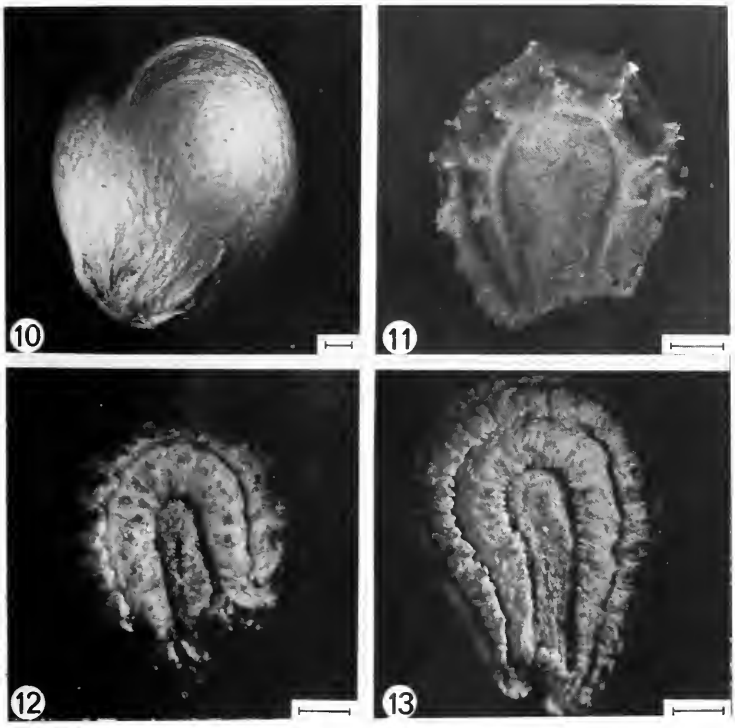

FIG. 10.
Albertisia delagoensis. Lateral view.

FIG. 11.
Stephania abyssinica. Lateral view.

FIG. 12.
Antizoma angustifolia. Lateral view.

FIG. 13.
A. miersiana. Lateral view.

Each scale division represents one millimetre.

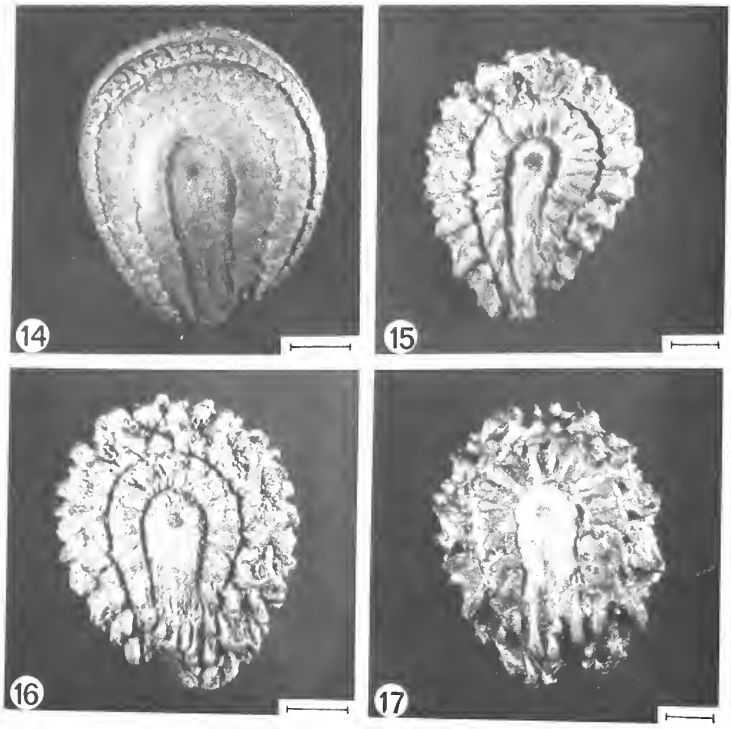

FIG. 14.
Cissampelos capensis. Lateral view.

FIG. 15.
C. hirta. Lateral view.

FIG. 16.
C. mucronata. Lateral view.

FIG. 17.
C. torulosa. Lateral view.

Each scale division represents one millimetre.

(ii) endocarp ellipsoidal with a flattened base and the condyle occurring as an enclosed globular cavity within the endocarp; and

(iii) endocarp horseshoe-shaped with the condyle linear, obovate or narrowly obovate.

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POLLEN DEVELOPMENT IN *TRITICUM DURUM* DESF.: A HISTOCHEMICAL STUDY

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Abstract

Pollen formation in the anther of *Triticum durum* Desf. was studied histochemically using Carnoy's fixed material and light microscopy. The substances localized were: DNA, RNA, proteins and ascorbic acid (AA) in the tissue sections and the content determined in different tissues.

Uittreksel

STUIFMEEL ONTWIKKELING IN *TRITICUM DURUM* DESF.: 'N HISTOCHEMIESE ONDERSOEK

Stuifmeel vorming in die helmknop van *Triticum durum* Desf. is histochemies met Carnoy-gefikseerde materiaal en ligmikroskopie ondersoek. Die stowwe gelokaliseer was DNA, RNA, proteïne en askorbinesuur (AA) in die weefselsnitte en die inhoud is vir verskillende weefsels bepaal.

Introduction

Although detailed morphological and cytological studies have been made on many important flowering plants, histochemical and physiological studies have been limited. Such studies, revealing the functions of different tissues of the anther, are now receiving considerable attention. In the present work an attempt has been made to substantiate the histochemical differentiation in the anther of *Triticum durum* Desf. during its successive ontogenetic stages. For this purpose, qualitative assessments of DNA, RNA, proteins and ascorbic acid were made employing standard histochemical methods on tissue sections in conjunction with light microscopy.

Material and Methods

Flower buds of *Triticum durum* Desf. fixed in Carnoy's medium were dehydrated in an ethanol–*n*–butanol series and embedded in paraffin. Serial microtome sections of 8 micron thickness were cut and mounted with gelatin adhesive.

RNA and DNA were localised using the azure B and Feulgen methods, respectively (Jensen, 1962). The following controls were run: RNA and DNA

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were extracted with 5% hot perchloric acid for 30 min at 60 °C (Erickson, 1949) (Fig. 14); RNA alone was extracted with 10% cold perchloric acid (Kasten, 1965) (Fig. 15). Total proteins were demonstrated using the mercuric bromophenol blue (HgBPB) reaction (Mazia *et al.*, 1953).

In order to localise ascorbic acid (AA) the following silver nitrate ($AgNO_3$) method was adopted (Dave *et al.*, 1968): fresh flower buds were immersed in a solution containing 34 mℓ 5% silver nitrate plus 66 mℓ 100% alcohol and 5 mℓ acetic acid and left for one week in the refrigerator. Later, the treated material was thoroughly washed in 50% ethanol and dehydrated as mentioned above. The paraffin sections were dried on the slides, deparaffinized in xylene and sealed with Canada balsam. Observations were made under the light microscope.

Results

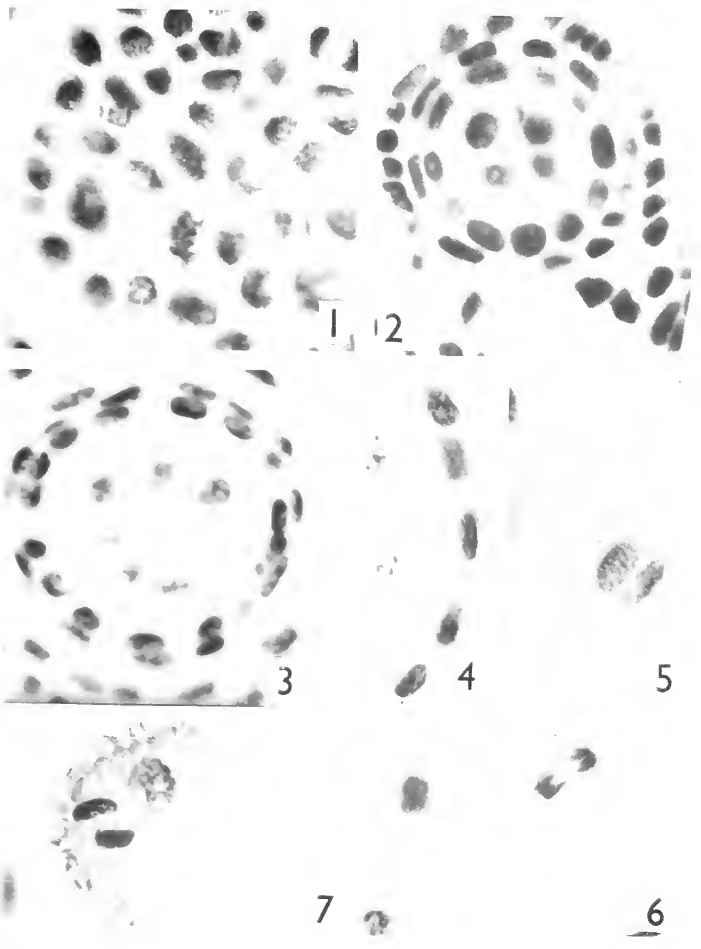
DNA: the hypodermal archesporial cell in the anther primordium appears to be rich in DNA, similar to the neighbouring cells (Fig. 1). In the early stages, the sporogenous tissue appears to be rich in DNA (Fig. 2) which decreases to a low level in the late stage (Fig. 3) and in the pollen mother cells. During meiosis-I a considerable increase in DNA content occurs at prophase. Although DNA is high at late anaphase-I, the resulting dyads and tetrads show low DNA.

After the separation of spores, the microspores in the resting phase contain low DNA (Fig. 4), while prior to mitosis, DNA again increases. Equal concentration of DNA occurs in both generative and vegetative cells (Figs 5, 6). Later, in the 2-celled pollen, DNA content in the generative cell increases again. In the mature 3-celled pollen, the male cells contain higher levels of DNA than the vegetative nucleus (Fig. 7).

In the course of entire anther development, the epidermal layer, endothecium and wall layers are rich in DNA (Figs 2, 3). When the PMC's are formed, the innermost wall layer functions as tapetum; its DNA content appears to increase to a high level (Figs 3, 4). This higher DNA content is maintained until it degenerates. In *Triticum*, binucleate tapetum is observed.

RNA: in the anther primordia, the archesporial cell is large and is rich in RNA (Fig. 8). The primary sporogenous tissue which is derived from the archesporium also retains a high concentration of RNA (Fig. 9). Later, the RNA level declines (Fig. 10) until ultimately, its level in the pollen mother cells is fairly low (Fig. 11). The nucleoli in all these phases are rich in RNA. The low cytoplasmic RNA level of the PMC's is continued during meiosis in the dyads and tetrads. The tetrads of spores are vacuolated; their nucleoli are rich in RNA (Fig. 12). During interphase an increase in RNA synthesis is observed; it is continued in the vegetative and generative cells of 2-celled pollen (Fig. 13).

Simultaneously with the differentiation of the sporogenous tissue, the primary parietal layer, which is rich in RNA, contributes to the endothecium. In the older anther, the endothecium and the epidermis, both of which were rich in RNA, show



FIGS. 1–7.
Anther sections of *Triticum durum* stained for DNA. Figs 1–3. Pre-meiotic stages showing high DNA levels in all the tissues, but low in the late sporogenous tissue in Fig. 3, X 400. Fig. 4. Post-meiotic stage. Note low intensity of DNA in the nuclei of microspores when compared to tapetum, X 600. Figs 5, 6. Mitotic divisions in the pollen grain showing relatively high DNA levels in both generative and vegetative cells, X 400. Fig. 7. 3-celled pollen, with the male cells, rich in DNA X 500.

a gradual fall in RNA content (Figs 10, 11). Similarly, the connective tissue also shows very low RNA. The tapetum synthesises RNA even at the connective side (Figs 10–12). In the mature anther, the endothecial layer develops wall thickenings which stain faintly green with azure B. Subsequently, the tapetum degenerates at the time of pollen formation, while maintaining its high RNA content.

Proteins: the young anther primordium is rich in proteins. Following the first parietal division in the archesporium the protein content of the nuclei of sporogenous cells is also high (Fig. 16). In the older anther, the sporogenous tissue is rich in cytoplasmic and nuclear proteins. During its further growth and differentiation into pollen mother cells, a sharp rise in protein content is observed (Fig. 17). The nucleoli also stain intensely for proteins. During meiosis-I, however, the cytoplasmic protein concentration seems to decline, while the proteins of spindles and chromosomes remain high (Figs 18, 19). This low cytoplasmic protein level is maintained during meiosis-II. At the time of microspore formation, the protein level increases again (Fig. 20). In the shedding pollen however, the male cells and the vegetative nucleus stain more intensely for protein than the cytoplasm (Fig. 21).

In the anther, as the wall layers differentiate, a decrease in protein content similar to that of RNA is observed. The reduction in the protein level occurs in the wall layers, centripetally with the successive differentiation of the latter. The epidermis also undergoes a decline in protein content. The glandular tapetum maintains a high concentration of proteins at all stages of anther growth (Figs 17–19).

Ascorbic acid (AA): Ascorbic acid is present in all the tissues of the anther. The young anther primordium stains uniformly for AA. No conspicuous distribution pattern of AA appears. However, in young sporogenous cells where only one parietal layer is differentiated, more AA appears in the latter (Fig. 22). The sporogenous tissue contains little AA; later, this tissue and tapetum appears to be richer in AA (Fig. 23), whereas the anther wall layers have a slightly lower AA content. In pollen mother cells a slight increase in AA synthesis occurs (Fig. 24). It appears to be more intense at the periphery of the cell walls and the nuclear membranes (Fig. 24). The same concentration is observed even at prophase and metaphase of the PMC's; the chromosomes stain a strong black. No additional synthesis takes place afterwards. At the tetrad stage, the spores show a peripheral

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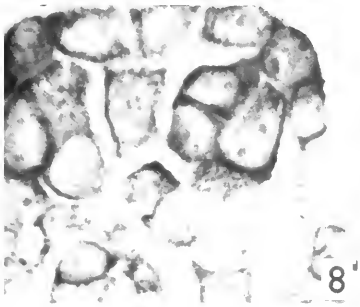
Figs. 8–15.

Anther sections of *Triticum durum* stained for RNA. Figs 8–11. Pre-meiotic stages showing high RNA content in the sporogenous tissue and tapetum; however, it declines in pollen mother cells at the onset of meiosis (Fig. 11). Note the gradual reduction of RNA in the anther wall layers, X 600; Fig. 11, X 500. Fig. 12. Microspore tetrad and tapetum respectively showing low and high RNA, X 700. Fig. 13. 2-celled pollen high in RNA in the generative and vegetative cells, X 900. Figs 14, 15. Control tests for RNA and DNA. Note both RNA and DNA (Fig. 14) and RNA alone extracted (Fig. 15), X 500.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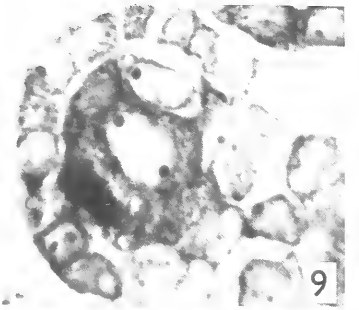
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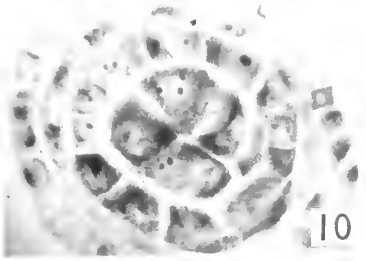
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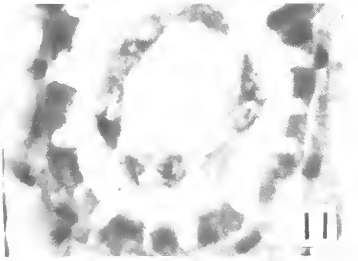
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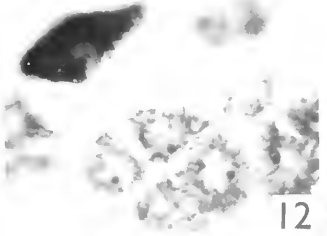
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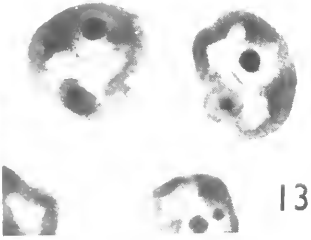
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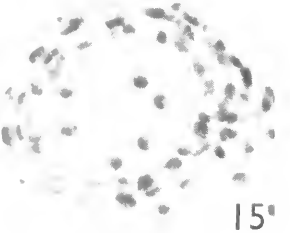
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deposition of AA (Fig. 25). The tapetum during meiosis resembles the PMC's in AA content, although its inner peripheral sheath contains more AA. The quantity and the mode of distribution of AA in PMC's is maintained in young microspores (Fig. 26). In 2-celled pollen, both vegetative and generative cells are rich in AA. The exine and intine are negative to the AA test. Mature pollen reacts similarly to 2-celled pollen. During meiosis the AA level in the anther wall layers is low; this is continued even at maturity.

Discussion

In general, correlation of growth patterns of different anther tissues appears to be simple when viewed morphologically, but not so when observed histochemically. Normally, the early growth of the anther primordia is dominated by cell division until the differentiation of the various tissues. Thus, the archesporium and sporogenous cells enter the phase of specialized cell growth and differentiation which culminates in the formation of pollen. During this period the tapetum acts as an accessory (nursing) tissue. The remaining tissues of the anther show a progressive decline in cell division and differentiate mainly in terms of cell expansion.

During early growth of the anther, the amount of DNA, as indicated by its staining intensity in the sporogenous tissue gradually declines; it increases again at the prophase of meiosis. The relatively low DNA content of the resulting dyads, tetrads and young microspores as compared to that of the tapetum and anther wall layers correlates with the fact that the latter tissues are diploid and the former are haploid. This, however, has not been the case with the diploid sporogenous nuclei, where a low DNA content appears to be a feature (Rudramuniyappa, 1973; Panchaksharappa and Rudramuniyappa, 1974, 1975). It should be kept in mind, however, that low DNA stainability in the nuclei may be due to interference by basic proteins, the histones (Heslop-Harrison, 1972). The histones probably mask staining of DNA. If this possibility is correct, the neighbouring maternal tissues of

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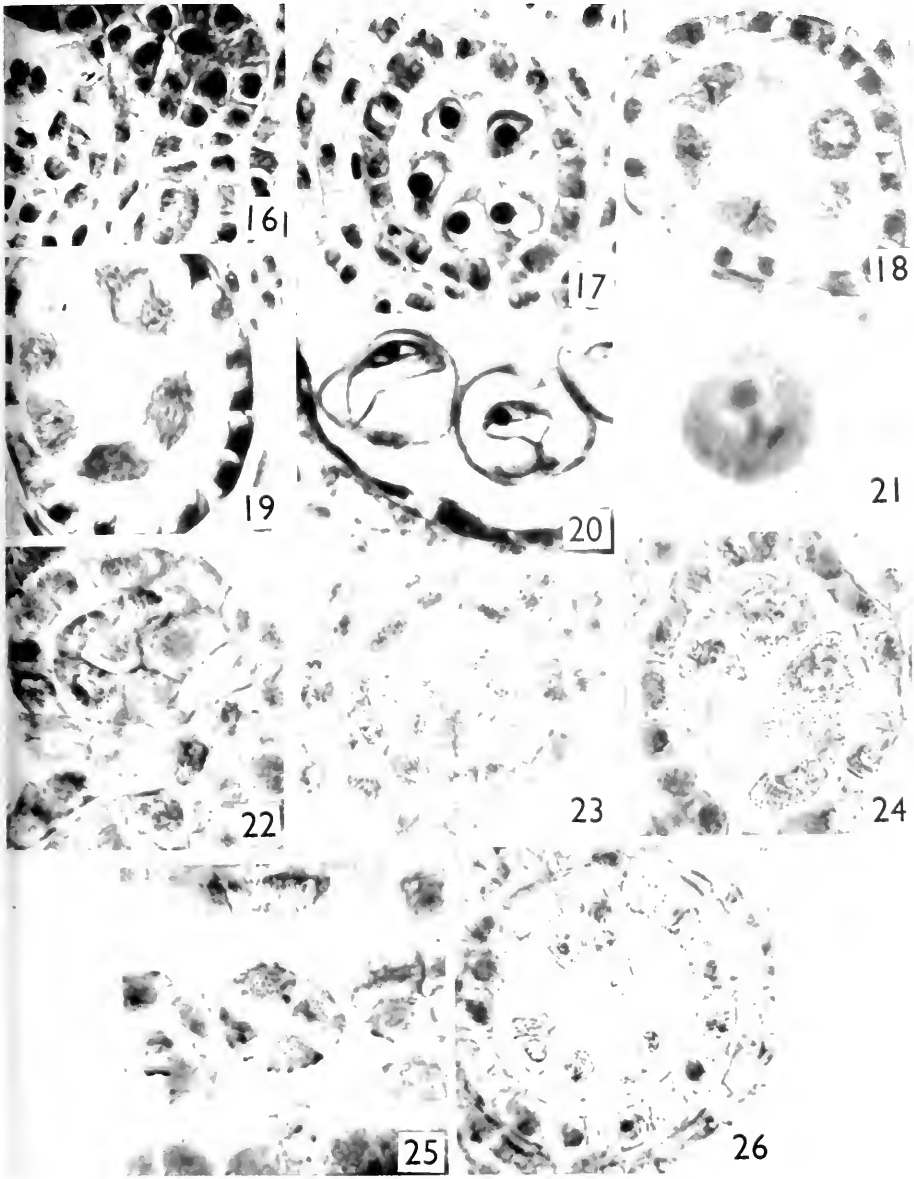
Figs. 16–26.

Anther sections of *Triticum durum* stained for proteins (Figs 16–21) and ascorbic acid (AA) (Figs 22–26). Figs 16, 17. Pre-meiotic stages showing high protein levels in the early sporogenous tissue, pollen mother cells and tapetum; note intense staining in the nucleoli, X600. Figs 18, 19. Meiosis. Note gradual reduction of proteins in the cytoplasm, but chromosomes and spindles are rich in proteins. Tapetum remains rich, but the wall layers are low in proteins, X 700. Figs 20, 21. One- and three-celled pollen respectively showing high protein levels in the cytoplasm, male cells and vegetative nucleus. Fig. 20, X 600; Fig. 21, X 800. Figs 22, 23. Pre-meiotic stages. Note the gradual synthesis of AA in sporogenous tissue and in newly differentiated tapetum (Fig. 23), X 700. Fig. 24. Pollen mother cells and tapetum synthesize AA; its location is mainly at the periphery of the cells, X 700. Figs 25, 26. Tetrad and young microspores, respectively showing a strong deposition of AA. Note the intensity of staining along the walls of the microspores and tapetum, X 700.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the anther which show a high DNA intensity might contain low levels of basic proteins.

RNA and protein synthesis in the meiocytes and their derivatives appears to be low when compared to that in the sporogenous tissue. Autoradiographic studies on *Lilium* (Taylor, 1959) and *Paeonia* (Sauter, 1968, 1969) have supported this observation in *Triticum*. However, during meiosis a reduction of AA has not been observed in either *Triticum* or in *Coix* (Bhatt and Shah, 1976). Generally, low concentrations of histochemically located substances in the cells or tissues suggest a low metabolic rate. Therefore, it appears that low rates of metabolism in the pollen mother cells may bring changes during meiosis. Alternatively, a low rate of metabolism in meiocytes, dyads and tetrads in *Triticum* and in some members of the Gramineae (Rudramuniyappa, 1973) may be due to the deposition of PAS-positive substance (callose) around them (Panchaksharappa and Rudramuniyappa, 1972), a universally occurring feature in all the plants investigated. This conclusion may be supported by the observation that at the pre-meiotic stage, the sporogenous tissues and at the post-meiotic stage, the pollen cells which are undergoing mitotic divisions show no such deposition of PAS-positive substances, hence they are rich in RNA, proteins and AA. It is possible that the dividing cells may be constantly utilizing and/or exporting materials with a consequent reduction in the concentration of histochemical substances. However, lack of synthesis of these substances at this juncture may also bring about a reduction in metabolism.

Male gametophyte: Next in importance to meiosis is the differentiation of pollen. The differentiation of the male gametophyte starts in the tetrad itself at the time the latter is undergoing a deposition of PAS-positive material. In *Triticum*, the spores in the tetrad show low concentrations of RNA, proteins and DNA. In most of the plants there is little or no RNA synthesis during the early stages of microspore development (Heslop-Harrison, 1972). However, as the microspore approaches mitosis, metabolism increases, as indicated by increased levels of RNA and proteins.

The AA grains are large and deposited at the periphery of the cytoplasm of the tetrads of spores. The presence of AA stimulates enzymes namely, amylase, catalase, lipase, protease and RNAase (Saxena *et al*., 1969). It appears that the enzymes concerned with carbohydrate metabolism may be involved in the breakdown of PAS-positive depositions, i.e., the polysaccharide material present around the tetrad of spores. The large AA grains of the tetrad have been degraded into smaller ones in the microspores and their distribution is still at the periphery. The peripheral distribution of AA in the tetrad and young microspores also seems to indicate that this substance plays a role in pollen wall formation.

In *Tradescantia* (LaCour, 1949) and *Paeonia* (Sauter, 1971), the vegetative cell is extremely active in synthesizing RNA and proteins, whereas the generative cell is inactive. Furthermore, in *Paeonia* the DNA-associated histones are higher in the generative nucleus than in the vegetative one. According to Heslop-Harrison

(1972), differences in RNA in vegetative and generative cells depends mainly on the density of ribosomes present. In *Triticum*, both the cells are active in synthesizing RNA, DNA, AA and even in 3-celled pollen they are rich in proteins and DNA. However, the DNA stainability of the vegetative nucleus of 3-celled pollen is low. The reason for such a low DNA content is not known. The mature pollen grains of the Gramineae are nutritionally independent, as they store abundant starch and lipids in addition to proteins, RNA and AA (Rudramuniyappa, 1973).

Tapetum: Much has been said regarding the nutritive role of this tissue, but no definite conclusions have yet been offered. In *Triticum*, the tapetum is secretory, being rich in RNA, DNA, AA and proteins whereas the pollen mother cells themselves contain low concentrations of these substances. Many studies have revealed the presence of high levels of DNA, RNA, proteins, AA and lipids (see Heslop-Harrison, 1972; Panchaksharappa and Rudramuniyappa, 1974, 1975; Rudramuniyappa, 1977) as well as submicroscopic organelles viz., ribosomes, amyloplasts and Golgi bodies (Marquardt *et al.*, 1968; Vasil and Aldrich, 1971; Echlin, 1971) in the tapetum. The presence of PAS-positive grains (not starch) has been recorded in the tapetum of maize and *Paspalum* (Panchaksharappa and Rudramuniyappa, 1974, 1975b). Its role in the anther is still open to question, as both sporogenous tissue and tapetum lack vascular connections and they appear side by side in the anther locule. Although many histochemical and electron microscopic studies on the tapetum reveal its metabolic and secretory nature, it is not known how these biochemical substances are secreted by this tissue. According to Heslop-Harrison (1972), the tapetum must function at least in a transmitting role in view of its location and the fact that it provides the only channel through which substances can reach the meiocytes, but there is no unequivocal evidence of transfer of these secreted products. Therefore, more direct evidence is required of its nutritional and/or translocation role.

Anther wall layer: Morphologically, the anther wall layer in the Gramineae consists of an outermost epidermis, an endothecial layer and a single middle layer. The latter disintegrates during meiosis. However, these layers exhibit very conspicuous histochemical changes (Heslop-Harrison, 1964; Milyaeva and Tsinger, 1968; Panchaksharappa and Rudramuniyappa, 1972, 1974, 1975a, b; Rudramuniyappa, 1977). It is believed that the various metabolites stored in the anther wall layers are utilised by the developing pollen (Rudramuniyappa, 1977). In the anther, RNA and proteins decline gradually as the successive wall layers differentiate, indicating that these substances are utilized during their early differentiation. At later stages of anther growth, when cell division has ceased, RNA and protein levels decrease, whereas DNA persists at a relatively high level. The anther wall layers play an important role in the nutrition of the anther, as indicated by the universal occurrence of plasmodesmata between these layers, the tapetum and

sporogenous tissue. However, at some stage of anther growth these connections become severed between the tapetal cells and pollen mother cells, whereas they persist between the latter (see Heslop-Harrison, 1972). Therefore, it is quite possible that the increase in the nutritive substances in the tapetum may be due to the contribution of anther wall layers by way of translocation through the plasmodesmata.

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THE EFFECT OF WATER STRESS ON THE NITROGEN METABOLISM OF TWO MAIZE LINES: 1. EFFECTS ON THE PROTEIN CONTENT AND RNASE ACTIVITY

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Abstract

The effect of drought conditions on the relative percentage water deficit, protein concentration and RNase activity was investigated in two maize lines. There seems to be a good correlation between protein content, RNase activity and drought resistance.

Uittreksel

DIE INVLOED VAN WATERSPANNING OP DIE STIKSTOFMETABOLISME VAN TWEE MIELIELYNE:
1. INVLOED OP DIE PROTEÏENINHOUD EN RNASE AKTIWITEIT

Die invloed van droogtetoestande op die relatiewe persentasie watertekort, proteïeninhoud en RNase aktiwiteit is by twee mielielyne ondersoek. Daar is blykbaar 'n noue verband tussen proteïeninhoud, RNase aktiwiteit en droogtebestandheid.

Introduction

Protein content of plants decreases during drought periods (Stutte & Todd, 1969; Savitskaya, 1972 and Dhindsa & Cleland, 1975). This is probably caused by the hydrolysis of proteins (Stocker, 1961) and an interruption of the protein synthesis system by a higher RNase activity (Arad & Richmond, 1976 and Maranville & Paulsen, 1972). There seems to be a good correlation between protein content and drought resistance. Drought-resistant plants have a higher protein content than plants with poorer drought resistance (Todd *et al.*, 1962). Estimation of protein content therefore might be an effective method for selection of drought resistance in plants (Stutte & Todd, 1967).

Material and Methods

Two maize lines, A281 and G556 DT, differing in drought resistance were used as experimental material. The plants were grown in controlled environmental cabinets in plastic pots of 150 mm diameter and with 3 kg of light red sandy loam as the root medium. Fertilizer (3:2:1) was added to the soil in the ratio of 1 g fertilizer to 1 kg of soil. The day length was 13 h, temperature 29 °C, the relative

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humidity 35 % and the light intensity 14 530 lux. Night temperature was 20 °C and the relative humidity during the night 40 %. After germination the plants were watered every second day with 200 mℓ water for 5 weeks. Thereafter only the control plants were watered as usual. Experimental samples were taken on the first, third, fifth and seventh day after the plants had last been watered. Ten plants of each maize line were cut off just above the ground and then cut into small pieces. Nine replicates of all the determinations were used.

Relative percentage water deficit (RWD) was estimated according to a method based on that of Stocker (1929). The RWD was calculated as follows:

$$\frac{\text{Turgor mass} - \text{Fresh mass}}{\text{Turgor mass} - \text{Dry mass}} \times \frac{100}{1}$$

Turgor mass of the tissue was obtained after the leaf segments had been floating on distilled water for 24 h.

Total water-soluble proteins were extracted according to a method based on that of Van Loon & Van Kammen (1968). One g of the leaf tissue was homogenised in 25 mℓ ice cold 0,1 M Tris (hydroxymethyl)-aminomethan buffer (pH 8,0). The extract was centrifuged for 15 minutes at 30 000 × gravity at a temperature between 0–2 °C. The supernatant was used for the determination of total water soluble proteins according to the method of Lowry, *et al.* (1951). Determinations on bovine serum albumin were used to plot a calibration curve.

The method used for the determination of RNase activity was based on the method used by Arad *et al.* (1973). One g of the leaf tissue was frozen in liquid air and then homogenised in 10 mℓ ice cold 0,1 M phosphate buffer (pH 6,0). The homogenate was centrifuged for 15 minutes at 15 000 × gravity at a temperature between 0–2 °C. One mℓ of the supernatant was added to 2 mℓ of substrate solution (yeast RNA 4 mg/mℓ in 0,1 M phosphate buffer pH 6,0) in test tubes. The assay mixture was incubated at 40 °C for 1 hour. Undigested RNA was precipitated with 1 mℓ of chilled 25 % perchloric acid containing 0,75 % uranyl-acetate. The tubes were left at 0–2 °C overnight and then centrifuged at 7 000 × gravity for 10 minutes. The absorbance of the supernatant was measured at 260 nm.

Results

The results in Figure 1 show a linear increase in the RWD of both maize lines with increasing water stress. The RWD of A281, however, was higher than that of A281 throughout the stress period. Especially from the third day onwards there was evidently a more rapid desiccation of A281.

Estimation of the water soluble protein content showed that G556DT had a higher content than A281. The protein content of both maize lines decreased from the first day, and especially from the fifth day onwards there is a rapid decrease

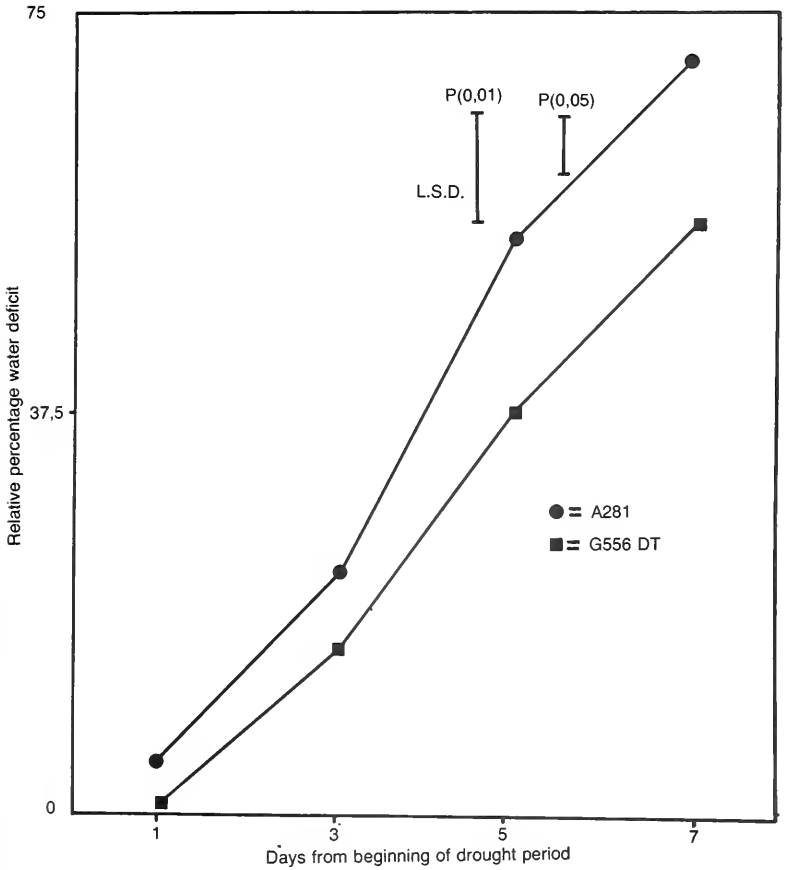

FIG. 1.
Changes in the relatative percentage water deficit of the two maize lines during a period of increasing water stress.

(Fig. 2). The percentage decrease, however, is much lower especially between day one and five, in G556DT than in A281 (Fig. 3).

A281 showed an increase in RNase activity from the first day of the drought period and a very high increase from the fifth day onwards. G556DT only showed an increase after the third day, and the RNase activity was lower in this line than that of A281 throughout the stress period (Fig. 4).

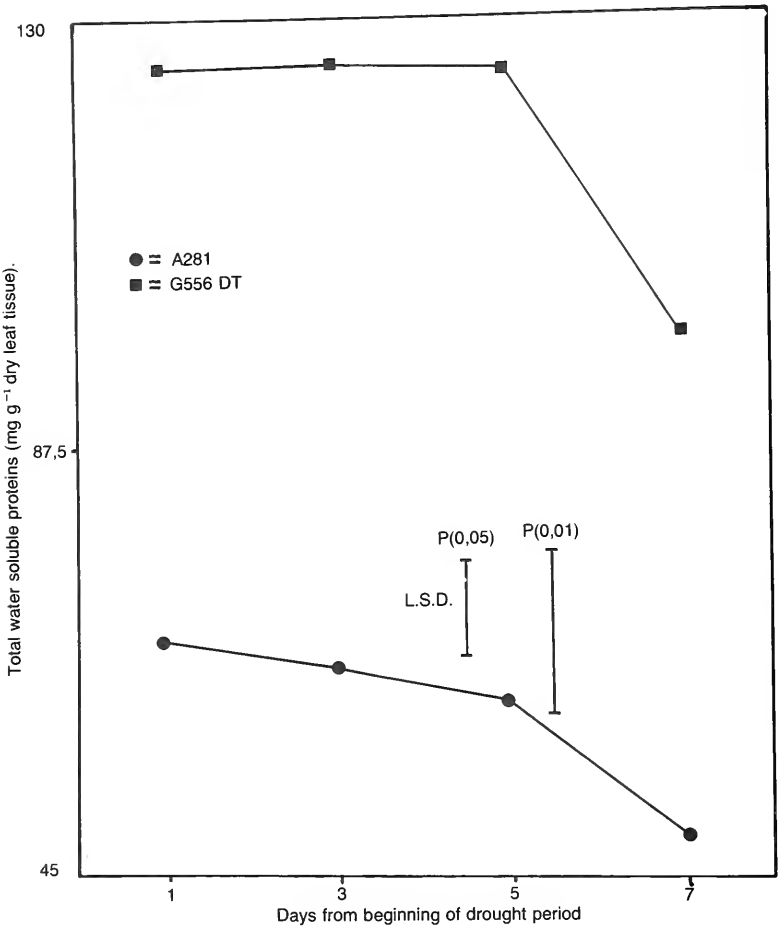

FIG. 2.
Changes in the total water soluble protein content (mgg^{-1} dry leaf tissue) of the two maize lines during the drought period.

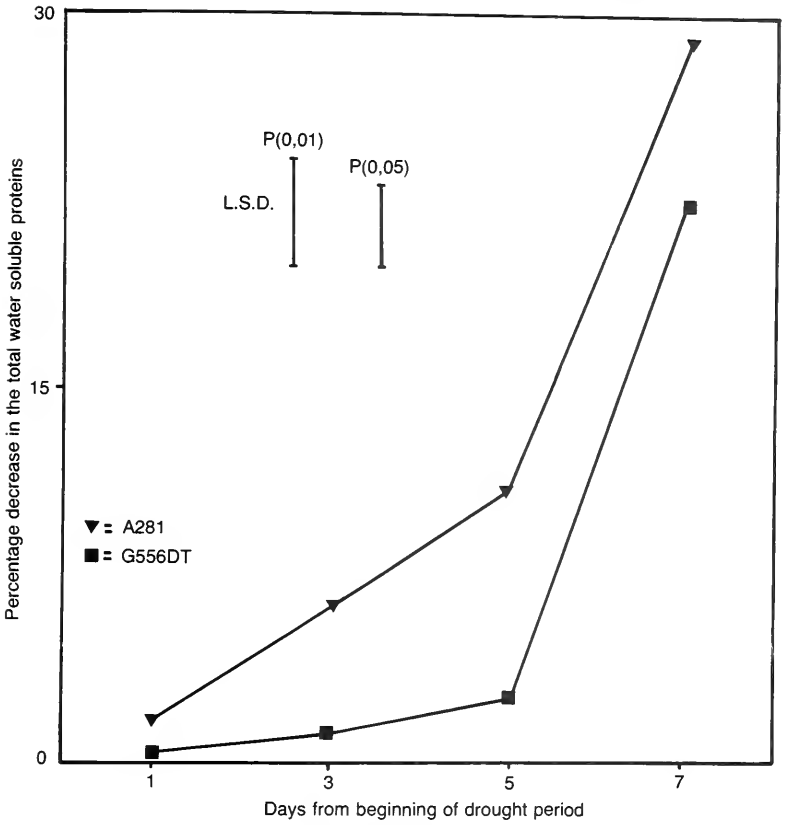

FIG. 3.
The percentage decrease in the total water soluble protein content during the drought period.

DISCUSSION

According to Chen *et al.* (1964) protein effects constitute the main component of the matrix potential of plant tissue. The higher water-soluble protein content of G556DT is probably the main reason why this maize line is able to delay the development of a water deficit in the tissue. Similar results to those reported in this communication were obtained by Todd *et al.* (1962), who found that wheat with high drought resistance had a greater protein content than wheat with a lower drought resistance.

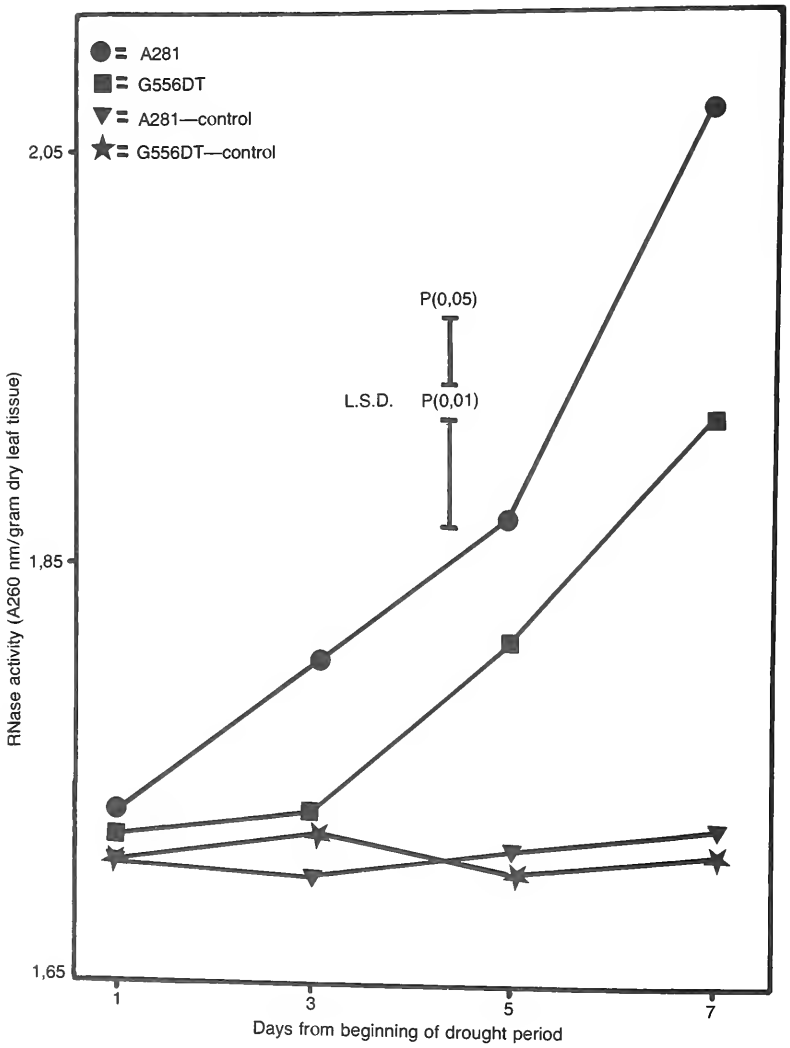

FIG. 4.
Changes in the RNase activity (A260 nm/gram dry leaf tissue) of the two maize lines during the drought period.

Conditions of water stress cause a decline in the protein content of both maize lines. Dhindsa & Bewley (1976), Maranville & Paulsen (1972) and Savitskaya (1972) also observed such decreases in protein content during drought conditions. It is, however, apparent that the decrease in protein content is smaller in G556DT than in A281, especially between days one and five (Fig. 3). This sharp decline in A281, is probably caused by the hydrolysis of proteins and a partial interruption of the protein synthesis system. Dehydration causes breakdown of the secondary and tertiary structure of proteins and this leads to an easier hydrolysis of the proteins (Chen *et al*., 1964).

One of the main factors affecting protein synthesis is RNase activity. The RNase activity evidently affects the rate of protein synthesis by destroying the mRNA linking the ribosomes (Henckel, 1970). In this experiment the increase in RNase activity is much higher in A281 than in G556DT throughout the water stress period, providing a possible explanation for the protein content differential between the two lines.

From the water deficit data it is evident that G556DT is more drought resistant than A281. This might be due to the higher protein content caused by the lower RNase activity during increasing water stress and possibly also by a more stable protein structure in the former maize line. Since the protein content of G556DT remained much higher than that of A281 throughout the periods of water stress, the results of this investigation support the idea that estimation of protein content may be a method for the selection of drought-resistant maize lines.

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SOME PRELIMINARY OBSERVATIONS ON THE SUBMERGED AQUATIC *ZOSTERA CAPENSIS* SETCHELL

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Abstract

The distribution of *Zostera capensis* along the South African coast and a morphological description of the plant is presented, together with some preliminary observations on laboratory germination and growth, and tolerance to changing environmental conditions.

These observations form the basis from which detailed research into vegetative and reproductive aspects of the growth cycle is being planned.

Uittreksel

VOORLOPIGE WAARNEMINGS VAN DIE ONDERWATERPLANT *ZOSTERA CAPENSIS* SETCHELL

Die verspreiding van *Zostera capensis* langs die Suid-Afrikaanse kus en die morfologie van die plant word behandel. Voorlopige waarnemings van ontkieming en groei in die laboratorium en verdraagsaamheid t.o.v. veranderende omgewingstoestande word bespreek.

Daar word beplan om toekomstige navorsing op die vegetatiewe en voortplantings siklus op die gegewens wat hier waargeneem is, te baseer.

Introduction

The submerged macrophyte *Zostera capensis* Setchell is the only known representative of the genus *Zostera* to occur in Southern Africa. Unlike its European and American counterparts, which appear as twelve distinct species, four of which are grouped in the subgenus *Zostera*, and eight in the subgenus *Zosterella* (Den Hartog), and which are now being subjected to intensive research, little is known about the life-cycle and phenology of *Zostera capensis*. Growing as it does in estuaries and intertidal mudflats, its importance lies not only in the shelter that it affords to a variety of organisms, but also in its availability as a nutrient source to the ecosystem, either as grazing or detritus. It has been accepted that seagrasses are highly productive, and it is probable that the primary productivity of *Zostera capensis* is comparable to the productivity of other seagrass ecosystems. *Zostera* is also thought to assist in the deposition of sediment carried under load, and acts as a sediment binding agent.

Like many seagrass localities of the world, our *Zostera* beds have been reduced by interference directly or indirectly attributable to man, and by deleterious environmental effects. Unfortunately, a fundamental lack of knowledge concerning the life-cycle of *Zostera capensis* has inhibited biological countermeasures being taken against this reduction, such as restocking programmes by

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transplantation and/or seed sowing. A continuation or increase in the imbalance which must already exist, will have a serious effect upon the many organisms so closely associated with *Zostera* and ultimately on the ecosystem as a whole.

The situation outlined above prompted investigations into the growth cycle and phenology of *Zostera capensis*, and this preliminary paper is an introduction to the plant, together with some phenological observations, both in the field and in the laboratory.

Distribution

Zostera capensis is widely distributed along the east coast of Southern Africa, from Inhaca Island (Moçambique) in the north to the Southern Cape (R.S.A.). Its known distribution along the west coast is limited to two localities, the northern limit being Saldanha Bay (Fig. 1). The localities listed under Fig. 1 are those at which *Zostera* has been recorded, but it is possible that the distribution may be wider than indicated. This suggestion is based on two criteria. Firstly, there has not been a systematic search along all the South African estuaries, and secondly, the ease of incorrectly assuming the absence of *Zostera* because of an absence of aerial components when, in fact, the population is experiencing a seasonal "die-back" of aerial shoots after flowering, so that only rhizomes remain buried in the substrate.

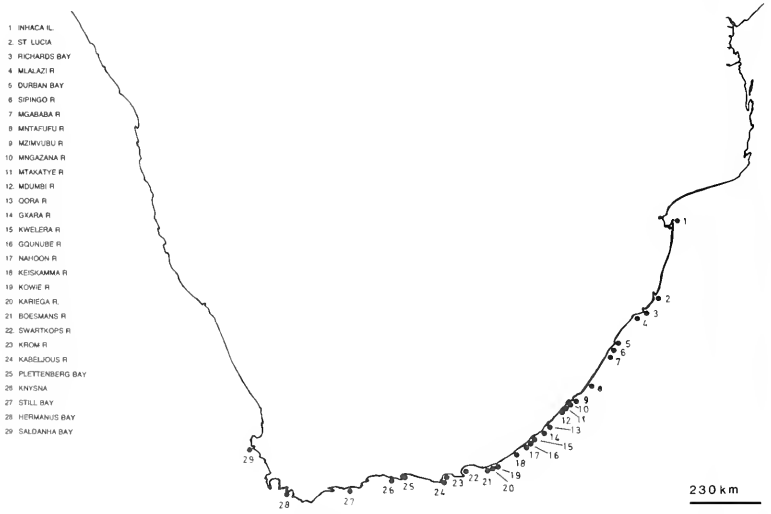

Fig. 1
Recorded distribution of *Zostera capensis* Setchell, along the east and south-west coasts of South Africa.

DESCRIPTION

The morphology of *Zostera capensis* has been described in detail by Setchell (1933), Obermeyer (1966) and Den Hartog (1970).

The plant has two vegetative components, (namely) a creeping rhizome system, and erect turions or leaves (Fig. 2). The rhizomes are 1–4 mm in

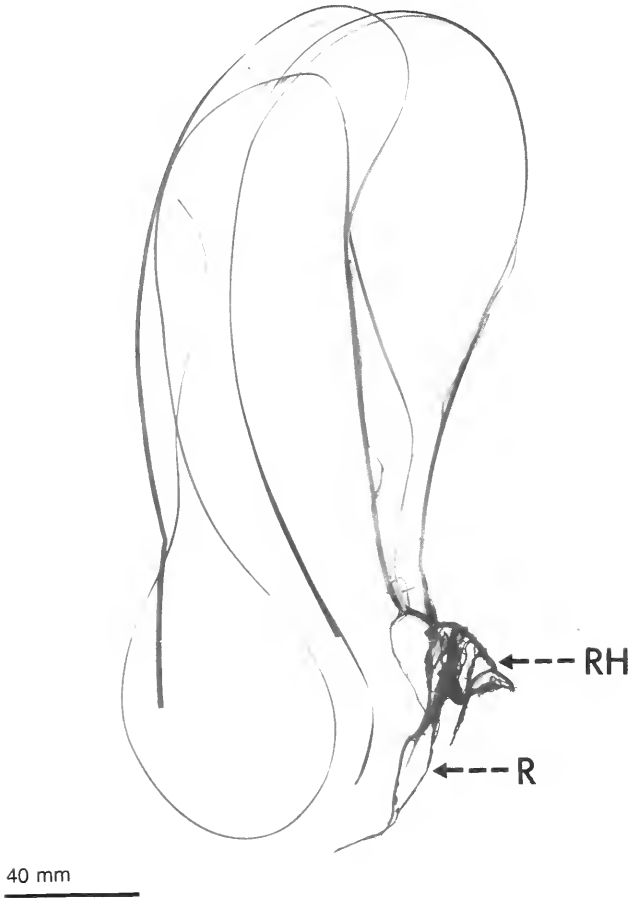

FIG. 2
Zostera capensis Setchell, showing unbranched roots (R), rhizome (RH) and erect turions.

thickness with internodes 4–30 mm in length. Nodes have up to five unbranching roots, with lengths of up to 100 mm.

The erect turion consists of a leaf sheath, flattened with two membranous lobes, and a lamina of variable length, usually to a maximum length of 300 mm, although plants growing in deeper water have been found with laminae of 900 mm (Steinke, pers. comm.). Lamina width is 1–3 mm.

There are three nerves on either side of the midrib, which run parallel to each other, except for the distal end of the lamina, where they converge towards the apex. Cross-veins occur at intervals and are either at an angle to, or perpendicular to the midrib. The lamina apex is obtuse or emarginate, becoming cleft with age.

The reproductive or generative shoots are erect, 1–2 mm in width, and give rise to a variable number of peduncles, alternately arranged. Each peduncle is terminated by a spadix enclosed in a membranous overlapping spathe. The spathes are 10–20 mm in length and up to 3 mm in width. The spadices contain 3–16 male flowers and 3–6 female flowers, arranged in two parallel rows, in such a way that a female flower occurs between two male flowers (Fig. 3). The male flowers are sessile, unilocular anthers (Fig. 4), while the female flowers consist of unilocular ovaries each containing a solitary ovule (Fig. 5), a style and two

FIG. 3
Young inflorescence with immature male and female flowers.

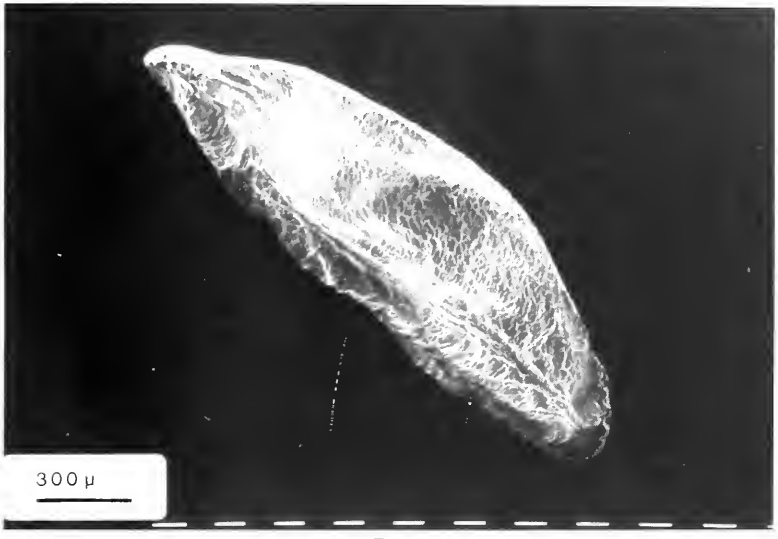

FIG. 4
The male flower, a sessile, unilocular anther.

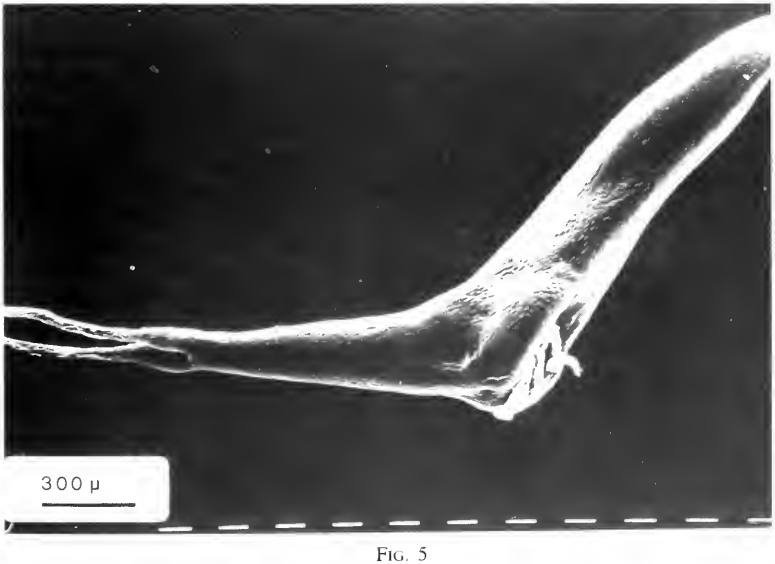

FIG. 5
The female flower consisting of two stigmatic arms, a style and a unilocular ovary.

stigmatic arms. The female flowers are protogynous. Pollen is filiform, and is produced in great quantities (Fig. 6).

Situated on the margins of the spadix at regular intervals are scale-like triangular structures, the retinacula (Fig. 7). The positions of these retinacula are such that each retinaculum subtends a group of flowers, composed of two male flowers and one female flower.

The seeds are ellipsoid, 2,6–3,0 mm in length, and have reddish-brown to black testas. The testas are characterised by longitudinal and fine transverse striations, and are resistant to pressure.

Plants having marked differences in leaf length have been found at a number of localities. It appears that plants growing in water shallow enough to allow regular exposure at low tides are generally short-leaved (maximum of 300 mm), while plants which are seldom, if ever exposed, have long leaves (maximum 900 mm). It is not known whether these morphological differences are due to genetic or environmental influences, and whether other phenotypic differences exist between the two forms.

Germination and Seedling Development

Germination of seeds, as observed in the laboratory, under continuous regimes of temperature (18 °C) and salinity (20‰) and a photoperiod of 12 hours, begins with the longitudinal splitting of the testa and gradual protrusion of the embryo.

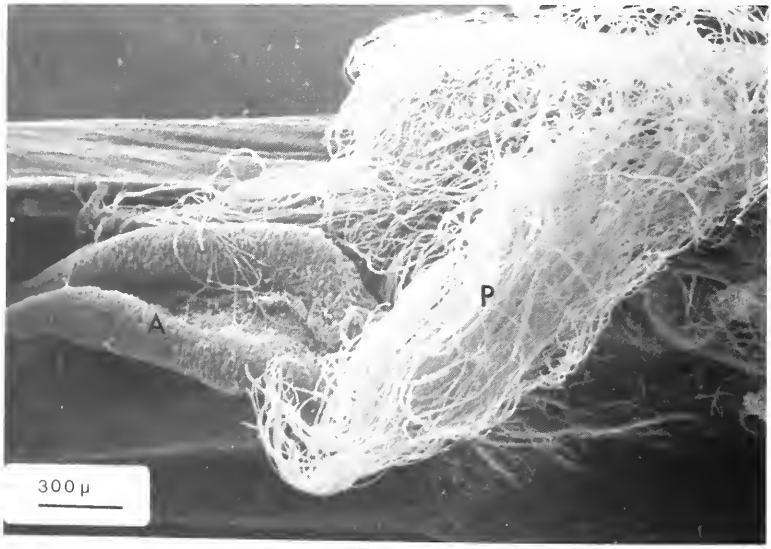

Fig. 6
A cloud of filiform pollen released from a dehiscent anther. P = pollen; A = anther.

FIG. 7
A retinaculum arising from the margin of the spadix.

The embryo is deeply grooved on one side, the groove corresponding to the longitudinal axis of the seed (Fig. 8). Terminating this scutellate embryo is a short hook-like structure, recurved towards the groove. Within the groove lies a cylindro-conic structure, which, as growth proceeds, increases in length, unfolds and protrudes from the embryo. It is suggested that the scutellate portion of the embryo is the cotyledon and the cylindro-conic structure the epicotyl. Concomitant with epicotyl development is the appearance of an outgrowth of tissue from a

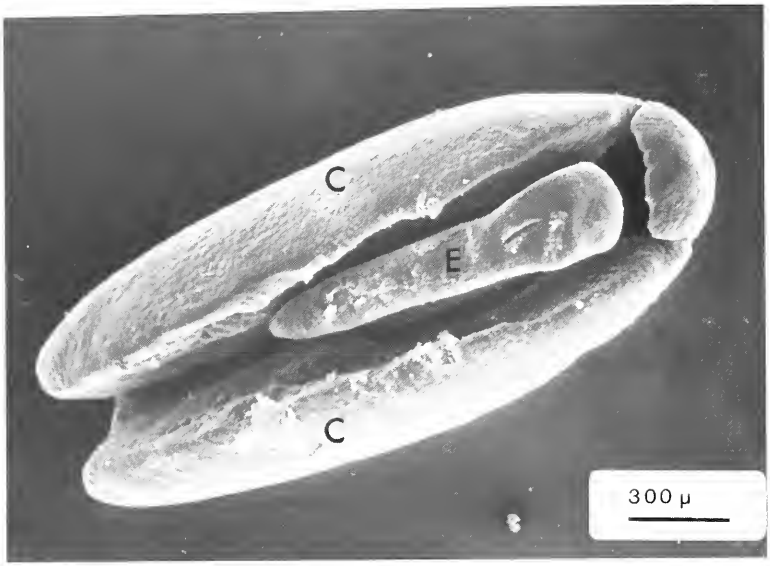

FIG. 8

Embryo composed of folded cotyledon (C) and trunk-like epicotyl (E).

point opposite the insertion of the epicotyl, and therefore opposite the cotyledonary groove. This outgrowth, described by Den Hartog (1970) as being a primary root common to subgenus *Zosterella*, is considered to be the radicle, by definition the rudimentary root of the embryo (Jackson, 1960). Its length increases to within a maximum of 20 mm (Fig. 9).

The epicotyl may vary in length, but is not usually longer than 20 mm. It is terminated by the first node, from which arise two or three lateral roots, and the plumule developing a fascicle of leaves, sheathed proximally by the coleoptile. By this stage of development the seedling is approximately three months old (Fig. 10).

Growth continues with increase in leaf-length and number and also in rhizome extension from the first node. Now leafy shoots arise from lateral and terminal buds, until after one year the plant consists of a branched rhizomatous system, with five to eight vegetative shoots and two or four reproductive shoots, which arise from terminal and lateral buds on the rhizome. The reproductive shoot can best be described as a rhipidium with two to five spathes (Den Hartog, 1970). The flowering period lasts about four months, and thereafter spathal decay and leaf senescence characterises a period in which growth is limited to the branching rhizome system.

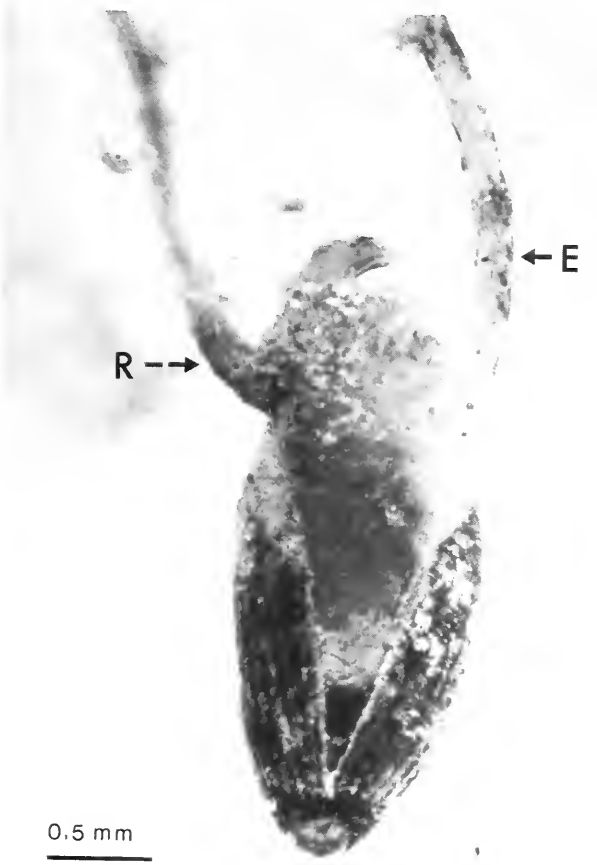

FIG. 9
Emergent seedling with the epicotyl (E) arising from the cotyledonary groove, and developing radicle (R).

The plants on which these descriptions were based are still under observation at the present time.

LABORATORY CULTIVATION AND TOLERANCE TO SOME ENVIRONMENTAL CONDITIONS

Preliminary investigations into the response of *Zostera capensis* plants to controlled artificial conditions have indicated a tolerance to transplantation and

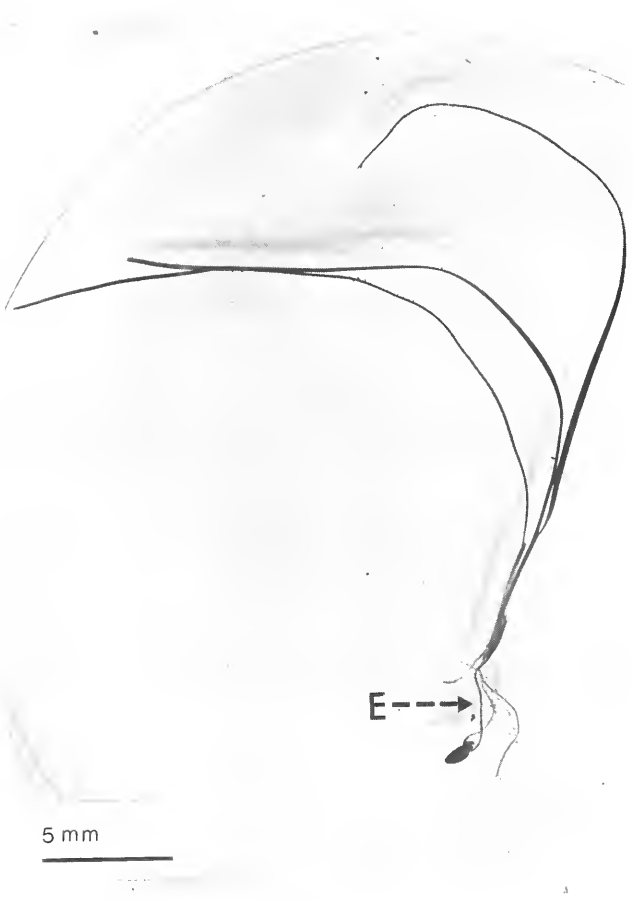

FIG. 10
A three month old seedling with well-developed fascicle of leaves and cotyledon still attached to the epicotyl.

environmental change, with the advantage that phenological investigations can be made in the laboratory, as a parallel to those made in the field. This tolerance to changing conditions is manifested not only in vegetative growth alone, but also to a certain extent in reproductive growth.

It is difficult in a preliminary investigation to ascribe specific growth responses and therefore tolerance levels to any particular environmental influence, since

these (growth responses) probably result from a combination or interplay of conditions over a certain period of time. However, it is possible to identify trends, indicating the direction in which detailed investigations will be made.

Substrate

Plants have been successfully transplanted into substrates of fine and coarse mud, and mixtures of top soil and compost soaked for a few days to remove suspended detritus. It is probable that *Zostera* will grow in most substrates, provided the organic content is sufficiently high. In the field this level is applicable only to initial colonization, since the shoots are efficient filters, aiding in the deposition of suspended particulate matter, in and around the beds.

While substrate requirements do not appear to be a limiting factor to laboratory culture, it is hoped that further investigations will provide information on plant/substrate relationships in the field.

Salinity

In the field, communities have been found in salinities ranging from 2‰ to 26‰. Salinity fluctuations at these localities have not been monitored over long periods, and the effects of rapid salinity changes in estuaries are not known.

In the laboratory, vegetative and reproductive growth has occurred in the salinity range of 15‰ to 30‰. Although a wide tolerance is indicated for vegetative growth, it is possible that the same may not be true for seed production. For example, maximum pollination may only occur within a narrow salinity range where the specific gravity of the medium is equal to that of the pollen. This could explain the low level of seed production obtained in the laboratory, even though there was sufficient agitation of the water body to ensure gentle movement of the pollen clouds. Whilst specific gravity differences may be of importance in an aquarium where the water body is comparatively still, just how limiting these would be in a fluctuating estuary is not known.

Temperature

In the laboratory good vegetative and reproductive growth has occurred in the temperature range of 15–20 °C. It appears that continuous exposure to temperatures of less than 10 °C and greater than 26 °C are limiting and result in a decreased growth rate. As far as can be ascertained, there does not appear to be a specific temperature range for vegetative or reproductive growth, as has been reported for eelgrass (Setchell, 1929; Boone & Hoeppel, 1976), and it is thought that temperatures may not be such an important controlling factor of reproduction. Further detailed investigation is required.

Photoperiod and light intensity

Plants subjected to photoperiods of 12–15 h grew well and flowered, as was expected since these periods correspond to field conditions when flowering has been observed. However, plants grown in a photoperiod of 6 h flowered as profusely as those in 12–15 h light regimes. It would appear that short photoperiods are not a limiting factor to vegetative or reproductive growth, provided light intensity remains above a certain level. Field intensity measurements and further investigations in the laboratory have yet to be done, but it is likely that low light intensity levels (eg. tidal action, turbidity, epiphytic shielding effects) result in very short-leaved forms with restricted reproductive growth. These observations are comparable to light intensity effects reported for eelgrass by Backman & Barilotti (1976), and reviewed by Boone & Hoeppel (1976).

Germination

Phillips (1976) reported field observations which indicate low germination rates of seagrass seed, and low success rates in the establishment of germinated seedlings. A low germination rate of *Z. capensis* seed has been obtained in this laboratory, with 4% of seed stored under ambient conditions (18 °C water temperature and 20‰ salinity) germinating after five months. Further germination occurred irregularly to give 15% germination after one year storage. Preliminary investigations involving differential treatments of salinity, temperature and light intensity have failed as yet to increase percentage germination. Testa removal resulted in limited epicotyl extension in some embryos, but these died after five weeks. It is not yet certain whether the low germination rate is due to low viability, quiescence imposed by adverse conditions, or some form of dormancy. Seeds have not been collected in sufficient numbers to enable viability and other relevant tests to be performed.

The transplantation of four-month old seedlings into aquaria where conditions were maintained as close as possible to those experienced in the field, viz. salinity 25‰, temperature 20 °C, substrate of fine mud, resulted in a 50% survival rate. The survivors grew vigorously and flowered 10 months after transplantation. There is no doubt that *Z. capensis* is amenable to transplantation into the laboratory, and whilst seedling mortality has been high so far, the establishment of older plants has been completely successful.

Biomass Determinations

Biomass determinations (standing stock in g/m^2) were initiated on a reduced, short-leaved population of *Z. capensis* in the Mlalazi Estuary, Zululand, with the average standing stock for a five month period being 60,26 g/m^2. This is low when compared with average seasonal maximum biomass ranges of eelgrass (*Z. marina*) of 97,55 g/m^2 to 1 463,24 g/m^2, and the average standing stock of eelgrass in the Izembek lagoon, Alaska of 243,88 g/m^2 (Boone & Hoeppel, 1976). Although

these plants are of a short-leaved type, it is probable that the low average standing stock is due in part to flooding of the Mlalazi River, which occurred during the sampling period. This work is being continued, together with biomass determinations at other localities.

Discussion

The preliminary phenological observations described above have been useful in establishing direction for detailed investigations into vegetative and reproductive aspects of the growth cycle. Germination of seeds in the laboratory enabled observations to be made on seedling growth and development, through the first flowering stage until spathal decay. Preliminary observations on responses to varying environmental conditions indicate that these plants are able to tolerate changes of salinity, temperature, photoperiod and light intensity. At this stage emphasis is being placed on gaining a greater understanding of flowering and germination stimuli, to enable plants to be cultivated in the laboratory over a number of generations.

The characteristic senescence of erect components of *Zostera* after flowering and seed development has been briefly mentioned (see Distribution). The frequency of growth, flowering and decay after seeding is in question, although some field observations indicate that profuse flowering as exhibited by a whole population at a given locality is a two year event. To what extent rhizome decay follows vegetative and reproductive decay is not known. It is hoped that careful monitoring of large field populations will clarify the situation.

Of particular interest is the elucidation of the state of the seed prior to germination. The terms quiescence and dormancy as previously used, need to be defined here, to ensure clarity of meaning. Quiescence is a state of arrested development maintained solely by unfavourable conditions, while dormancy is a state of arrested development imposed by the organism itself. The germination rate of 15% for seeds stored at a temperature of 18 °C, and a salinity of 20‰ for one year suggests the possibility of dormancy rather than quiescence where one would expect an all or none process, that is, no germination or a high rate of germination. It may be that these seeds have slow and differential rates of embryo maturation, coupled with a low viability. Extensive tests have been planned to investigate this phenomenon.

It has been suggested by Phillips (1976) that seagrasses may develop physiological races due to local climatic conditions and that transplantation into new geographic localities may require a period of acclimation. As far as *Z. capensis* is concerned, material for laboratory cultivation has been collected from Zululand and the Eastern Cape, and growth responses have indicated an ability to adapt to certain environmental changes without the need for acclimation. This suggests that the climatic differences experienced by the plants are within a tolerance range where growth is not noticeably affected after transplantation.

Acclimation may be necessary for plants collected from and transplanted into more diverse environments, but to what extent this would be successful is not known.

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THE GENUS *EUGENIA* L. (MYRTACEAE) IN SOUTHERN AFRICA: 1. THE NATURE AND TAXONOMIC VALUE OF THE FIRST-FORMED STEM PERIDERM*

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ABSTRACT

The nature of the first-formed stem periderm of some *Eugenia* species of Southern Africa was examined. Both the quantitative and qualitative characteristics of this tissue were evaluated for their taxonomic importance. This was done on the basis of a review of the known taxonomic value of the periderm with special reference to its application in the Myrtaceae.

A number of periderm characteristics were found which support the division of the species into two distinct groups. The most important of these is the position in which the periderm originates in the stem. From this it can be concluded that the first-formed stem periderm initiates either in the cortex (Group X) or in the primary external phloem (Group Y). This characteristic is correlated with two structurally different types of phellem and proves to be constant for a species. The identity of species with a hitherto vague taxonomic position, could be ascertained by checking the position in which the periderm originates in the type specimens.

The grouping of specimens based on periderm characteristics, closely agrees with the revision of Dümmer (1912). It does, however, not support the delimitation of some of the taxa as proposed by White (1977) in the most recent revision of the genus *Eugenia* in Southern Africa.

UITTREKSEL

DIE GENUS *EUGENIA* L. (MYRTACEAE) IN SUIDELIKE AFRIKA: 1. DIE AARD EN TAKSONOMIESE BETEKENIS VAN DIE EERSTE GEVORMDE STINGELPERIDERM

Die aard van die eerste gevormde stingelperiderm van 'n aantal *Eugenia*-spesies uit Suidelike Afrika is ondersoek. Beide kwantitatiewe en kwalitatiewe kenmerke van hierdie weefsel is vir hul taksonomiese waarde geëvalueer. Dit is gedoen in die lig van 'n oorsig van die reeds bekende taksonomiese waarde van die periderm met besondere verwysing na die toepassing daarvan in die Myrtaceae.

'n Aantal peridermkenmerke wat die verdeling van die spesies in twee verskillende groepe ondersteun, is gevind. Die belangrikste hiervan is die posisie in die stingel waar die

* This paper is based on results included in a thesis submitted by the first author to the Department of Botany, Potchefstroom University for C.H.E., in partial fulfilment of the requirements for the degree Magister Scientiae.

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periderm ontstaan. Hiervolgens kan die eerste gevormde stingelperiderm òf in die korteks (Groep X) òf in die primêre eksterne floëem (Groep Y) ontstaan. Hierdie kenmerk is met twee struktureel-verskillende tipes felleem gekorreleer en blyk konstant te wees vir 'n spesie.

Deur die posisie van peridermvorming by die tipe-eksemplare te kontroleer, kon die identiteit van spesies waarvan die taksonomiese posisie tot nog toe vaag was, vasgestel word.

Daar is gevind dat die groepering van eksemplare volgens peridermkenmerke nou ooreenstem met die hersiening van Dümmer (1912), maar nie die omgrensing van sommige taksons soos voorgestel in die jongste hersiening van die genus *Eugenia* in Suidelike Afrika (White, 1977), ondersteun nie.

1. Introduction

The genus *Eugenia* L. is one of the largest woody genera in the world (Good, 1969) and taxonomically one of the most difficult taxa to deal with. There are few other genera that confront the taxonomist with so many problems. One of these is the lack of useful and reliable external morphological characteristics which may be used to distinguish between the hundreds of described species.

This is also the case with the *Eugenia* species of Southern Africa where many herbarium specimens cannot be identified.

As an introduction to a revision of *Eugenia* in Southern Africa, an anatomical study of the leaf and stem has been undertaken (Van Wyk, 1978). One of the objectives was to evaluate a number of anatomical characteristics as an aid to the identification of taxa and to use such diagnostic characteristics to determine the identity of hitherto vaguely known species. It is the aim of this paper to describe and evaluate some characteristics of the first-formed periderm in the stem, and to discuss some of its taxonomic implications. Before evaluating the periderm characteristics it is necessary to briefly review the known taxonomic value of this tissue with special reference to its application in the Myrtaceae.

In comparative anatomical studies characteristics of the bark or rhytidome rather than only those of the periderm, are usually used. Despite the diagnostic appearance of the external surface pattern of the bark of many woody plants, not much effort has been made to correlate it with the internal structure (Whitmore, 1962 (a), (b) and (c)). The work of Douliot (1889) according to Carlquist (1961) nevertheless already contains systematically arranged information on the site of periderm initiation for a large number of genera. In a revision of the genus *Eugenia* s.l. in Malaya, Henderson (1949) stressed the large diagnostic value that the bark of this genus possess in field studies.

According to Lignier (1887, 1890) the phellem of the Myrtaceae consists of layers of radially flattened cells with thin or sclerified walls alternating with radially elongated thin-walled cells. The cell walls of the radially flattened cells are not suberised and are known as phelloids (Esau, 1965). Van Tieghem (1904) according to Solereder (1908) showed that the cell-shape of the different layers can also be the reverse of Lignier's results. Phellem consisting only of cubical thin-

walled cells occurs in some species of *Eucalyptus* and *Syzygium* (Metcalfe & Chalk, 1965).

The first-formed periderm in the stem of the Myrtaceae usually either originates in the parenchyma cells of the cortex or in the primary external phloem to the inside of the extraxylery ring of fibres (Blyth, 1958)—also called the pericycle (Lignier, 1887; Metcalfe & Chalk, 1965). According to Lignier (1887) the method of decortification is one of the more constant stem characteristics of the Myrtaceae that can be used for the purpose of identification. Although this characteristic is of value for the recognition of genera and subgenera (Solereder, 1908) it is important to bear in mind that the first-formed periderm is always more superficial than successive periderms (Metcalfe & Chalk, 1965). Metcalfe and Chalk (1965) also question the taxonomic value of the exact position in which the periderm originates (e.g. superficial or deep in the cortex). For the genus *Eugenia* the position in which the periderm originates can vary according to the species (Metcalfe & Chalk, 1965).

As examples of bark studies in the Myrtaceae the works of Brögli (1926) on *Eucalyptus* and *Eugenia* and Chattaway (1955 (a), (b), (c), 1959) on *Eucalyptus,* deserve mentioning. Chattaway (1953) found that the first-formed periderm coincides to a large extent in more than 150 *Eucalyptus* species. The nature of the rhytidome, however, was taxonomically important and could be used for the identification of species in which external morphological features show great similarity. It has further been found that the grouping of species according to bark characteristics supported a reclassification of species based on morphological characteristics.

The division of the *Eugenia* species of the Old and New World into two separate groups on the basis of wood anatomy (Dadswell & Ingle, 1947), is confirmed by the anatomy of the bark (Chattaway, 1959). This division supports the proposed classification of Merrill and Perry (1938 (a), (b), (c), 1939) which is also supported by other characteristics (Pike, 1956; Schmid, 1972).

The many periderm characteristics that can be used in comparative anatomy [Solereder, 1908; Chattaway 1953, 1955 (a) + (b); Carlquist, 1961; Whitmore, 1962 (a)] are usually very constant and are little influenced by external environmental factors. In this regard Bamber (1962) found that the characteristics of the bark of the Leptospermoideae are of greater taxonomic value than those of the wood of the same group.

Little is known about the seasonal activity and control over the initiation of the phellogen (Zimmerman & Brown, 1974). In this connection the work of Waisel, Lipschitz and Arzee (1967) shows that the phellogen can possess a seasonal rhythm that does not necessarily coincide with that of the vascular cambium.

2. Material and Methods

Both dried and preserved material have been used. Material from different

localities was selected to determine possible environmentally induced variation. Where possible plants of a particular species from at least five different localities were studied quantitatively to determine intraspecific variation. All material was identified by the first author according to the criteria used by Sonder (1862), Engler (1899), Dümmer (1912), Brown (1912), Engler and von Brehmer (1917), Strey (1972) and Van Wyk (1979).

The species discussed in this paper as well as the number of specimens of each species that were examined are given in Table 1. The names of the collectors and the collectors' numbers for the examined specimens can be found in Van Wyk (1978).

Dried material from herbarium sheets was rehydrated by transferring it to distilled water in which it was slowly heated and then boiled for about 30 minutes. Fresh and rehydrated material were fixed in formalin-acetic acid-alcohol (Johansen, 1940).

Fixed material was dehydrated with an ethanol-*n*-propanol-*n*-butanol series and infiltrated and embedded in a monomer mixture of purified glycol methacrylate or unpurified hydroxyethyl methacrylate (HEMA) (Feder & O'Brien, 1968).

Sections 2–4 μm thick were cut with a glass knife on an ultra-microtome and stained with toluidine blue or with periodic acid—Schijff (PAS) stain with

TABLE 1.

Species and number of specimens examined. (Species are grouped according to the results of the study. An asterisk indicates that type material of the species was also studied anatomically)

Species	Number of specimens examined quantitively	Total number of specimens examined
GROUP X		
**Eugenia capensis* (Eckl. + Zeyh.) Sond.	5	30
**E. gueinzii* Sond.	—	1
E. cf. *mossambicensis* Engl.	4	19
**E. natalitia* Sond.	6	40
**E. rudatisii* Engl.	—	1
**E. simii* Dümmer	3	19
GROUP Y		
**E. albanensis* Sond.	—	20
**E. erythrophylla* Strey	5	22
E. pusilla N.E.Br.	—	1
**E. verdoormae* Van Wyk[1]	5	10
**E. woodii* Dümmer	—	15
**E. zeyheri* Harv.	2	11
**E. zuluensis* Dümmer	3	11

* [1]Previously referred to as *E.* sp. nov. (Van Wyk, 1978).

toluidine blue as a counterstain (Feder & O'Brien, 1968). Schijff's reagent was prepared according to the method in Gurr (1963).

After staining with toluidine blue, sections of material embedded in unpurified HEMA were treated according to the method used by Ruddel (1967).

Freehand sections of fixed material were made to check the constancy of some characteristics for a species. For the localisation of lignified tissue and the periderm the phloroglucinol/hydrochloric acid method was used (Radford, Dickison, Massey & Bell, 1974).

The presence of tannin and suberin was shown with ferrichloride and Sudan IV respectively (Johansen, 1940).

Only transverse sections through the internodes of the stem were made.

Measurements were taken with an eyepiece micrometer. For practical reasons, a maximum of thirty readings per section were made for a specific characteristic. The mean of these readings is often affected by the few very low or high values that may occur. The median is however often a more representative value (Sokal & Rohlf, 1969), and was thus used in this study.

The size and wall thickness of the phellem and phelloid cells were measured as follows:

(a) Phellem cells:
The tangential and radial diameter were respectively measured between the outer edge of the two radial and tangential cell walls of thirty adjacent phellem cells on the same sections. In most cases the first or second row of phellem cells from the phellogen was used. At the same time the maximum thickness of the inner tangential walls was noted.

(b) Phelloid cells:
Measurements were made in the same way as in the case of the phellem cells. Usually the youngest row of phelloids in which the walls of the phelloid cells showed maximum thickness, was used.

Preference was given to those areas on a section where the thickest lignified walls occurred.

3. Results

3.1 *Nature of the periderm*

A periderm is initiated at an early stage in the development of the stem of all the species investigated.

The phellogen and phellem are easy to distinguish, but the phelloderm is poorly developed, usually consisting of a single layer of radially flattened thin-walled cells which are tanniniferous.

The phelloderm shows little variation in all the species and it has not been investigated quantitatively.

The phellem is characteristically that of the Myrtaceae (Metcalfe & Chalk, 1965) and possesses phelloids in which usually only the inner tangential and

radial walls are strongly thickened and lignified. As a result the phelloids appear horseshoe-shaped in cross section. These sclerified walls are usually, but not necessarily always, present in all the phelloids. They are particularly poorly developed in the older phelloid layers of *E. zuluensis* (Fig. 16). Lamellae can usually be distinguished in the thickened walls (Fig. 15). Most often a layer of phellem cells alternates with a layer of phelloids. Multiserial phelloid areas, however, are present in parts of the periderm of some specimens (Fig. 8).

Both the phellem cells and phelloids may be filled with tannin (Fig. 9). Radial phellem rays, one or more cells wide, of thin-walled and sclerified cells, are often present in the phellem (Fig. 14).

Although some lenticels were present on a few slides, especially in those of *E. capensis*, their nature and taxonomic value have not been investigated.

Structurally the periderm of the Southern African *Eugenia* species indicates an affinity with the *Eugenia* species of the New World (*Eugenia* s. str.; Chattaway, 1959).

3.2 *Origin of the periderm*

On the basis of the position in which the first periderm originates in the stem, the *Eugenia* species of Southern Africa can be divided into two groups. These two groups will be referred to as Group X and Group Y (Table 1; Fig. 1).

In Group X the phellogen originates in the parenchyma of the cortex, immediately below the epidermis. No decortification occurs as a result of this periderm (Fig. 6).

In Group Y the phellogen originates in the primary external phloem parenchyma, immediately inside the extraxylary ring of fibres (pericycle) (Figs 11 and 12). The cortex and epidermis shrivel shortly after the formation of the first layer of phellem cells and are pushed off together with the fibre ring (Fig. 13). Especially in freehand sections, older secondary phloem can be confused with the cortex because of the absence of the fibre ring in some specimens. However, secretory cavities are characteristically present in the cortex, but absent from the secondary phloem.

In order to determine the constancy of this characteristic, a number of specimens of most species have been investigated. Where possible, material obtained from the type specimens has been included. From these results it appears that the position in which the periderm initiates in normal stems is constant for a species.

In the same stem, under abnormal conditions, the phellogen can develop in two different positions (Fig. 10). This has been recorded in a specimen of Group X in which part of the superficial layers of the cortex was damaged. In

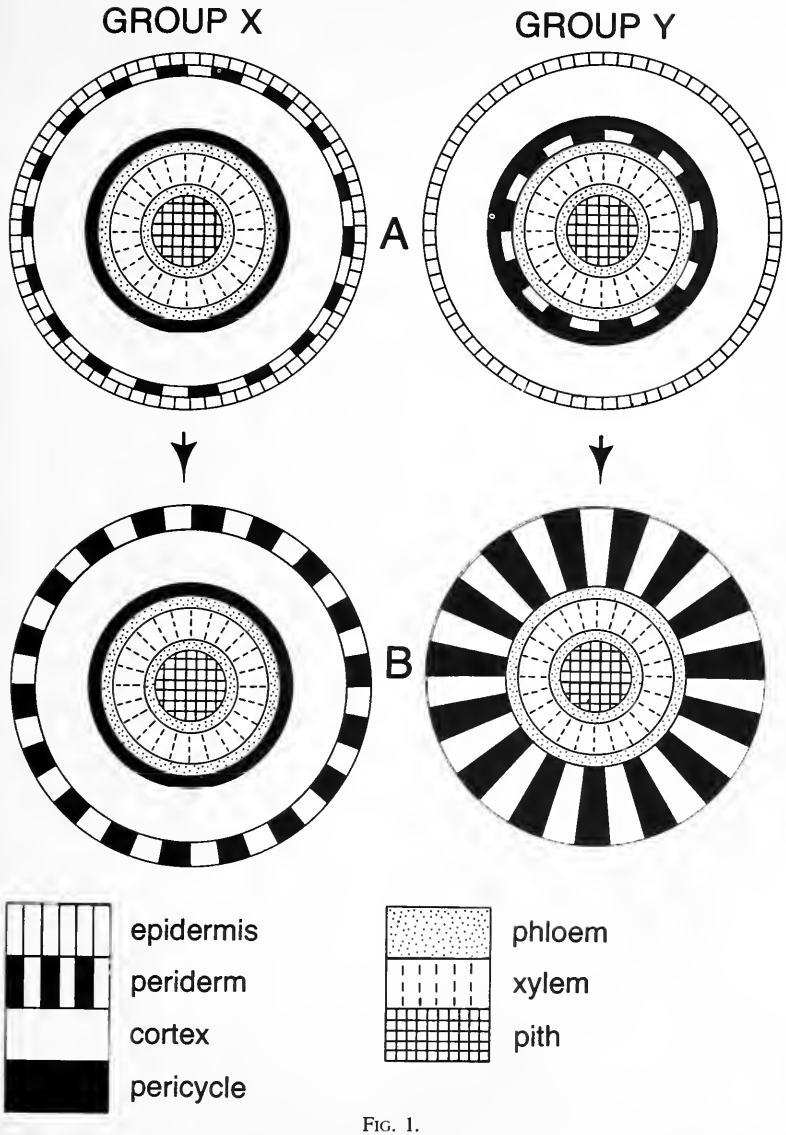

FIG. 1.
Line drawings of stems in transverse section to show the position of the periderm and distribution of the principle tissues in the two species groups which are distinguished. Group X = Periderm superficial in cortex. Group Y = Periderm in primary external phloem. A: Young stem; B: Older stem.

this specimen the periderm is continuous and develops partly subepidermally in the cortex and partly in the primary external phloem—the latter part opposite the damaged cortex.

3.3 *Nature of the cells in the phellem*

3.3.1 Phelloids

In Fig. 2 a scatter diagram is used to correlate the median of the tangential diameter of the phelloids with the median of their radial diameter. From this diagram it seems that the *Eugenia* species can be

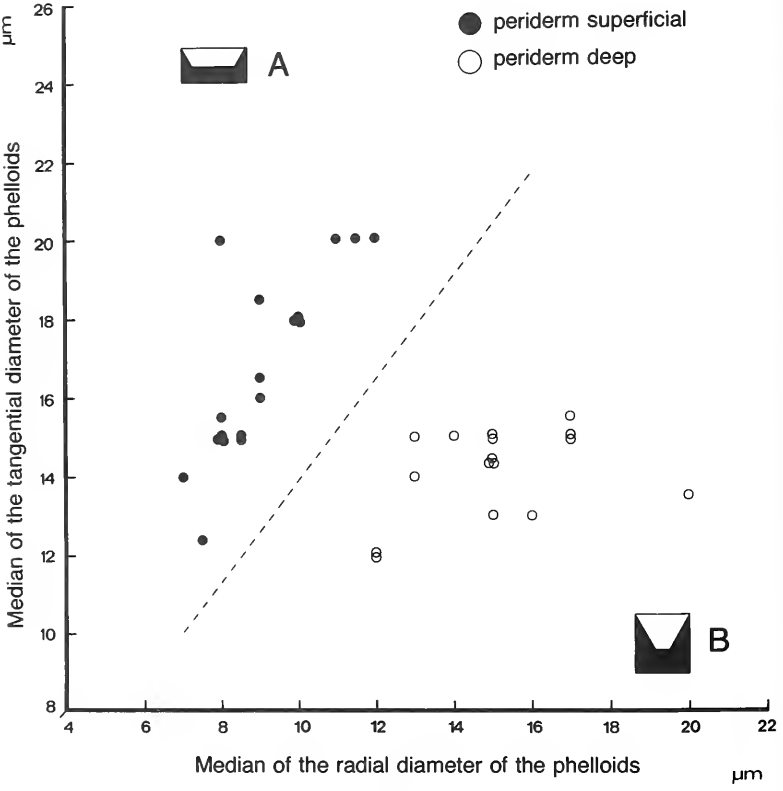

FIG. 2.
Scatter diagram to correlate the radial and tangential diameter of the phelloids. The schematic presentation of the phelloids (A + B) is according to scale and based on the mean of all the median values.

divided into two groups. This division correlates with the position in which the periderm originates. Species belonging to Group X possess phelloids which are radially flattened (Figs 7 and 8) while those of Group Y are radially elongated (Figs 14 and 15). The inner tangential cell walls of Group X are also more thickened than those of Group Y (Figs 7, 8, 14 and 15).

It is further noticeable that the thickened cell walls of Group X are more persistent than those of Group Y. Cell walls of the last mentioned group are often already delignified, or in a state of disintegration in the third phelloid layer from the phellogen (Fig. 15).

Numerous pits are present in the lignified walls of Group X (Fig. 9), while in Group Y they are usually poorly developed (Fig. 15). Lignified cell walls in sections stained with PAS/toluidine blue turned dark red in the case of Group Y but stained lightly in Group X. This may indicate possible differences in the chemical composition of the walls.

The size and wall thickness of the phelloids show little interspecific variation.

The mean of the cell diameter and wall thickness of the median values of the various observations has been separately calculated for all the specimens of Group X and Y and is shown in Table 2.

TABLE 2.
Size of the phelloids. (The mean and standard deviation of the values used in Fig. 2 & Fig. 4)

	Group X	Group Y
Tangential diameter	17,03 ± 2,15 μm	14,16 ± 1,12 μm
Radial diameter	9,15 ± 1,40 μm	15,06 ± 2,09 μm
Thickness of inner tangential walls .	3,76 ± 0,90 μm	5,96 ± 2,23 μm

3.3.2 Phellem cells

According to Fig. 3 it seems that the size of the phellem cells also supports the division of the *Eugenia* species into two groups.

Phellem cells of Group Y are radially flattened, while in Group X they are radially elongated. The median value of the tangential diameter is much the same in both groups. No prominent interspecific differences were noted.

The cell walls of Group X are slightly thicker than those of Group Y.

The values in Table 3 represent the mean cell size and wall thickness calculated from the median values of all the different measurements for all the specimens of Group X and Y.

TABLE 3.
Size of the phellem cells. (The mean and standard deviation of the values used in Fig. 2 & Fig. 3)

	Group X	Group Y
Tangential diameter	16,68 ± 2,84 μm	14,83 ± 1,74 μm
Radial diameter	16,65 ± 3,04 μm	9,20 ± 1,47 μm
Thickness of walls	1,41 ± 0,48 μm	1,0 ± 0 μm

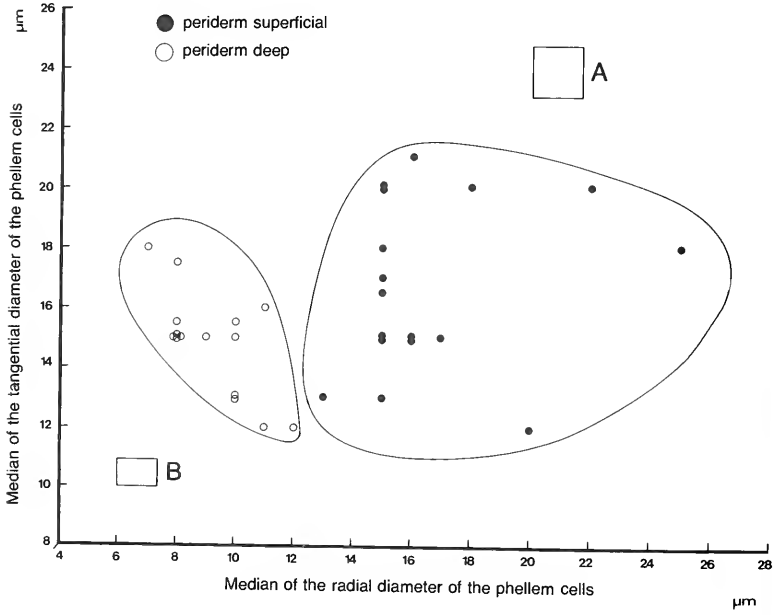

FIG. 3.
Scatter diagram to correlate the radial and tangential diameter of the phellem cells. The schematic presentation of the phellem cells (A + B) is according to scale and based on the mean of all the median values.

3.3 *Structure of the phellem*

The radial diameter of the phellem cells and phelloids is shown by means of a scatter diagram in Fig. 4.

In Group X layers of radially elongated phellem cells alternate with layers of radially flattened phelloid cells. The reverse applies to Group Y. The phellem structure is schematically shown in Fig. 5.

The two different positions in which the periderm originates are thus both correlated with a peculiar structural type of phellem (Figs 7, 8, 14 and 15).

4. Discussion

From a practical viewpoint the position in which the periderm originates is of great taxonomic significance. This characteristic has been investigated in a large number of specimens and was constant for a species. By checking this characteristic in the type specimens the identity of species with hitherto vague taxonomic

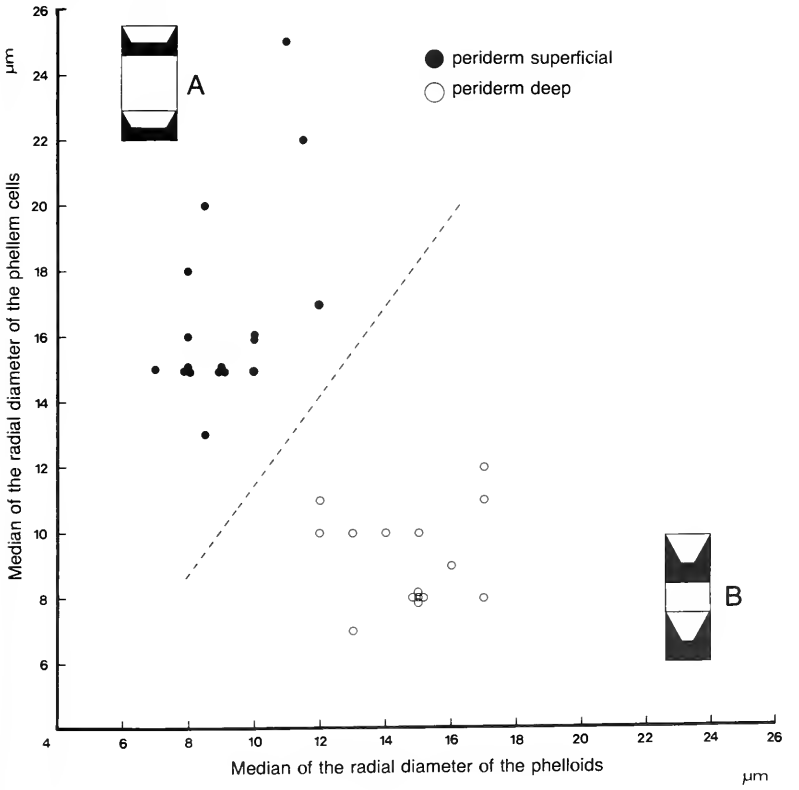

Fig. 4.
Scatter diagram to correlate the radial diameter of the phellem cells with the radial diameter of the phelloids. The schematic presentation of parts of the phellem (A + B) are according to scale and based on the mean of all the median values.

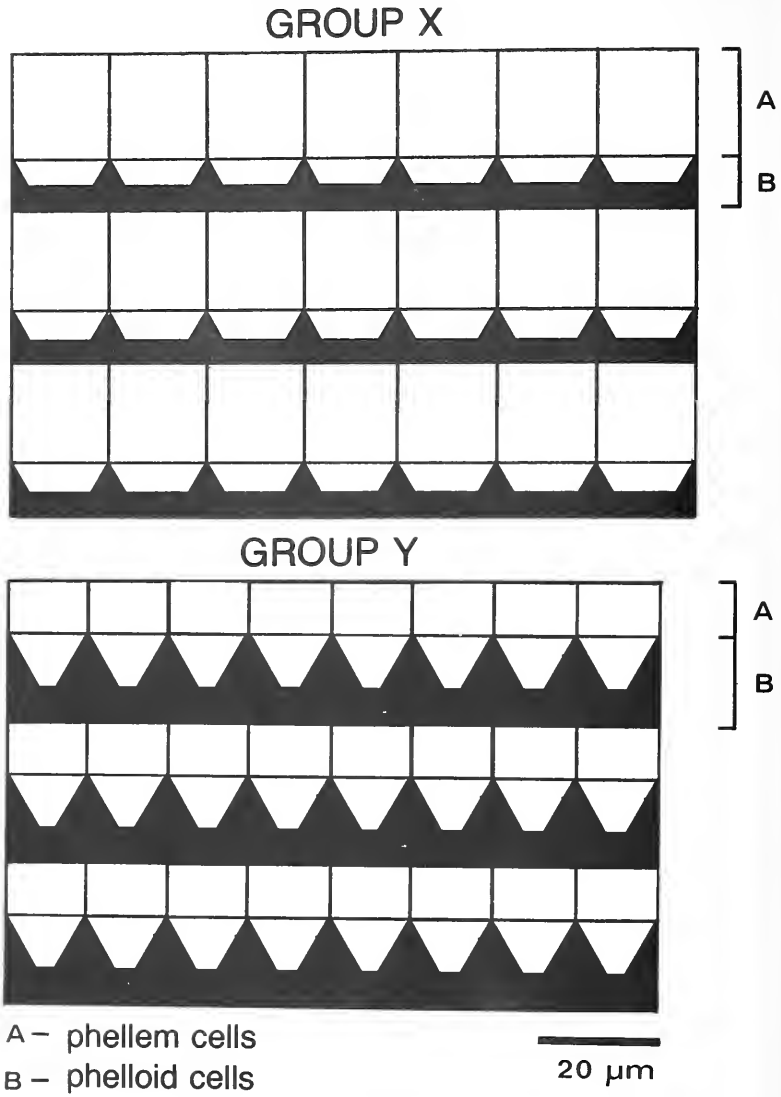

FIG. 5.
Schematic presentation of the structure of the phellem of the first-formed stem periderm in the two species groups; based on the mean values in Tables 2 and 3.

position could be determined. As an example the delimitation of some of the taxa proposed by Dümmer (1912) and White (1977) will next be discussed (Table 4). Taxa which, according to their periderm, belong to Group Y are in CAPITAL letters.

TABLE 4.

A comparison between the treatment of some Southern African *Eugenia* species by different authors. (Taxa belonging to Group Y are in CAPITALS)

Dümmer (1912)	White (1977)
Eugenia capensis (Eckl. + Zeyh.) Sond.	*E. capensis* subsp. *capensis* = *E. capensis*
E. natalitia Sond.	*E. capensis* subsp. *natalitia* (Sond.) F. White = *E. natalitia*
E. WOODII Dümmer	= *E. WOODII*
E. ZULUENSIS Dümmer	= *E. ZULUENSIS*
E. simii Dümmer	*E. capensis* subsp. *simii* (Dümmer) F. White = *E. simii*
E. ZEYHERI Harv.	*E. capensis* subsp. *ZEYHERI* (Harv.) F. White = *E. ZEYHERI*
E. ALBANENSIS Sond.	*E. capensis* subsp. *ALBANENSIS* (Sond.) F. White = *E. ALBANENSIS*
The brackets indicate that *E. simii* and *E. WOODII* have since the revision been confused with *E. ZEYHERI* and *E. natalitia* respectively.	This is a list of only some of the proposed new name combinations and their synonyms. Some of the taxa are described in Coates Palgrave (1977) and White (1978).

After the type material of all the species of Dümmer mentioned in Table 4 have been anatomically investigated the following conclusions with regard to the two classifications can be made.

Dümmer proves to be correct in his distinction of *E. natalitia* (Group X) and *E. WOODII* (Group Y) as two separate taxa. Such is also the case with *E. simii* and *E. ZEYHERI* which belong to two different groups.

According to White (1977) *E. ZULUENSIS* and *E. WOODII* are synonyms of *E. capensis* subsp. *natalitia* (=*E. natalitia*).

This is contradicted by the periderm study according to which the first two species belong to Group Y, while *E. natalitia* belongs to Group X.

With regard to the subspecies of *E. capensis* distinguished by White, it is possible that *E. simii* and *E. natalitia* should be allocated subspecific ranks. However, according to the periderm results, *E. ALBANENSIS* and *E. ZEYHERI* belong to Group Y and cannot be treated as subspecies of *E. capensis* (Group X).

If these two species are in fact of subspecific rank, it must be from a species in Group Y.

The above examples illustrate the practical value of the observed periderm characteristics. These characteristics are in fact supported by some other anatomical and morphological characteristics.

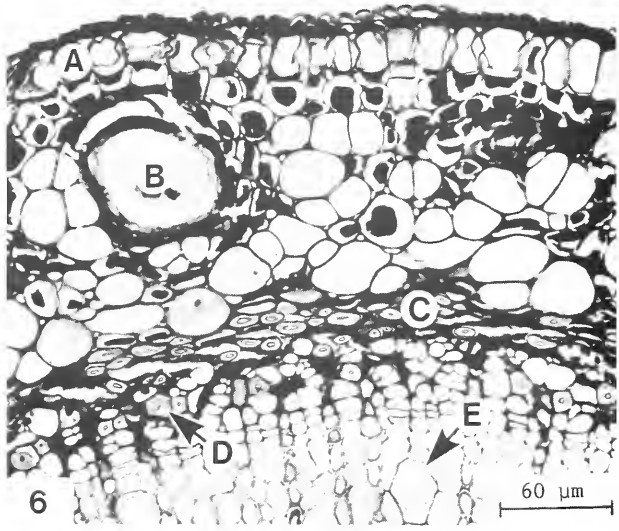

FIG. 6.
Transverse section of the stem of *E. natalitia* to illustrate the periderm (A) which is initiated subepidermally in the cortex; (B) secretory cavity; (C) pericycle with fibres; (D) sclereids in external phloem; (E) crystal bearing idioblast in secondary xylem.

5. CONCLUSIONS

The most important differences between the first-formed stem periderm of Group X and Y are summarised in Table 5. By using the phloroglucinol/hydrochloric acid test on freehand sections of fresh or rehydrated material the nature of the periderm can be ascertained in a quick and easy way. In the herbarium this method is indispensable in order to distinguish between species such as *E. simii* and *E. zeyheri* as well as *E. natalitia* and *E. woodii* which were confused in the past.

It is recommended that the nature of the periderm (especially position in which it is initiated) be investigated for all other members of the genus *Eugenia*. This might prove to be a considerable aid in the identification of specimens which are otherwise often confused.

TABLE 5.
A summary of the expression of some periderm characteristics in the two species groups which are distinguished.

Characteristics	Group X	Group Y
1. Periderm position	superficial in cortex	primary external phloem
2. Phellem cells	radially elongated	radially flattened
3. Phelloids	radially flattened	radially elongated
4. Phelloid walls	3,76 ± 0,9 μm thick	5,96 ± 2,23 μm thick
5. Pits in phelloid walls	numerous	few
6. Nature of thickened walls	relative stable	disintegrate soon after sclerification
7. Thickened walls stained with PAS/toluidine blue	stain dark red	show little staining

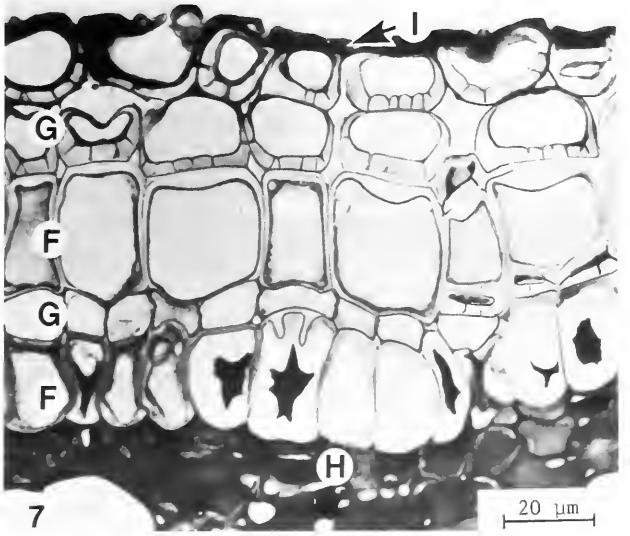

FIG. 7.
Transverse section of the stem of *E.* cf. *mossambicensis* to show the structure of the periderm. (F) radially elongated phellem cells; (G) radially flattened phelloid cells with thickened walls; (H) phellogen; (I) epidermis.

6. ACKNOWLEDGEMENTS

The authors wishes to thank the Director and Staff of the Botanical Research Institute in Pretoria for assistance provided in various ways. The financial aid received from the South African C.S.I.R. is acknowledged with thanks.

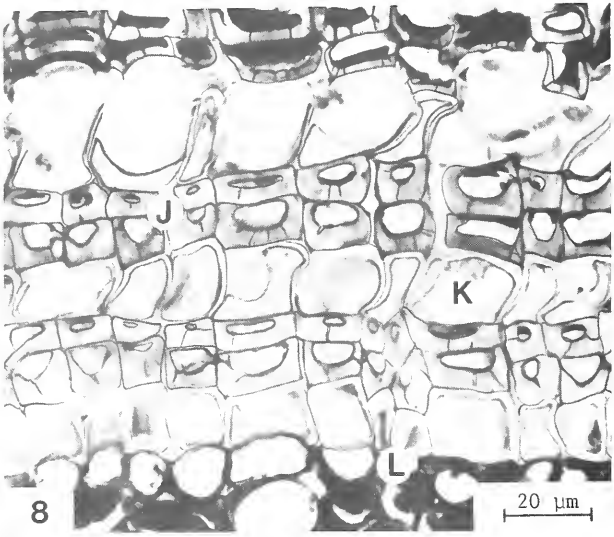

FIG. 8.
Structure of the stem periderm of *E. capensis* as seen in transverse section. Two layers of phelloids (J) alternate with single layers of phellem cells (K). (L) phellogen.

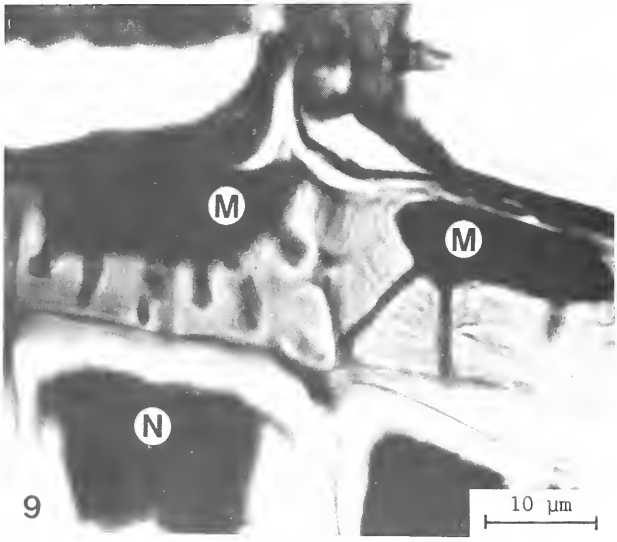

FIG. 9.
Transverse section of the stem periderm of *E. natalitia* to show the numerous pits in the thickened walls of the phelloids (M) which are tanniniferous. (N) phellem cell.

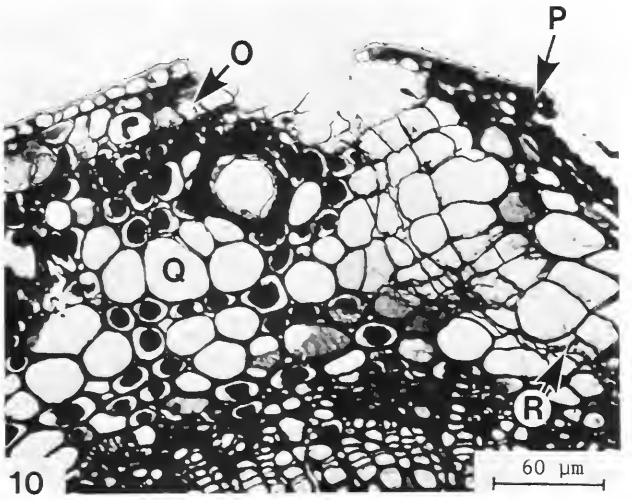

FIG. 10.
Transverse section of the stem of *E. natalitia* to show the superficial phellogen (O) which develops also in the primary external phloem (R) and deeper layers of the cortex (Q) if the superficial cell layers of the stem are damaged (P).

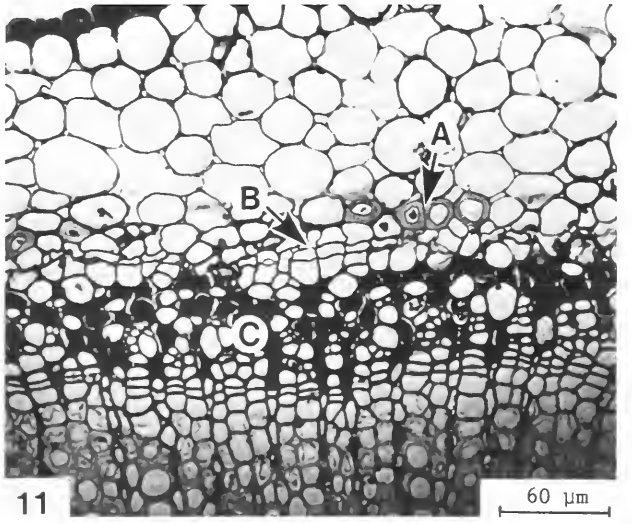

FIG. 11.
Transverse section of the stem of *E. albanensis* to show the initiation of the phellogen (B) in the primary external phloem inside the extraxylary fibre ring (A). (C) secondary external phloem.

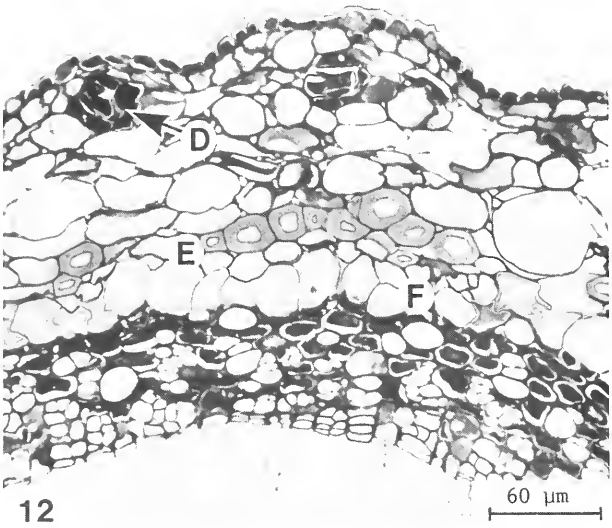

FIG. 12.
Transverse section of an older stem than in Fig. 11 of *E. albanensis* to illustrate the deep seated periderm (F). (E) extraxylary fibre ring; (D) secretory cavity in the cortex.

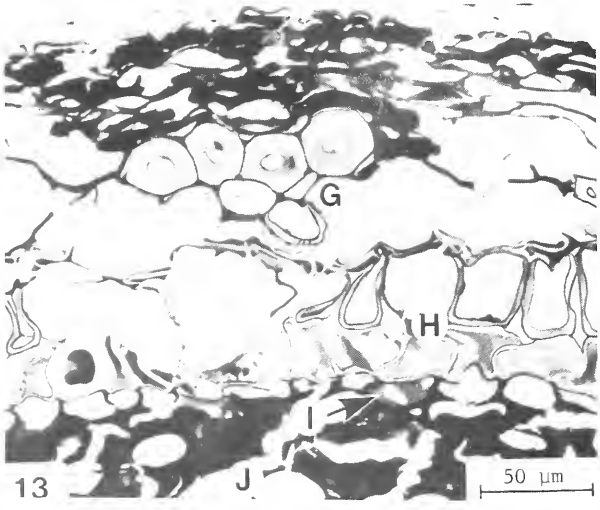

FIG. 13.
Transverse section of the stem of *E. albanensis* to show the decortification as a result of the periderm (H) in the external phloem (J); (G) extraxylary fibres; (I) phellogen.

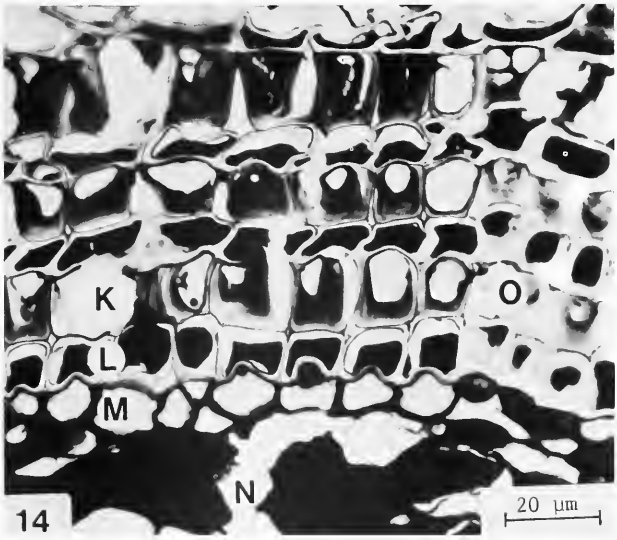

FIG. 14.

Transverse section of the stem periderm of *E. verdoorniae* to illustrate the structure of the periderm. (K) radially elongated phelloids; (L) radially flattened phellem cells; (O) phellem ray; (M) phellogen; (N) secondary external phloem.

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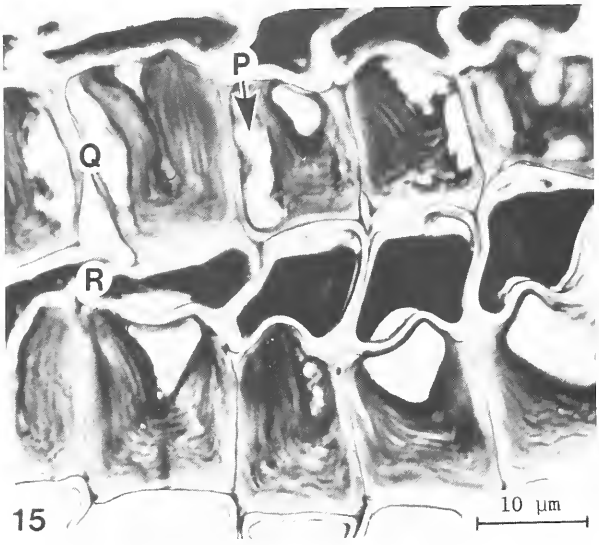

FIG. 15.

Transverse section of the phellem of *E. verdoorniae* to show the layering of the thickened phelloid (Q) walls. These walls disintegrate (P) in older phelloids and show no prominent pits. (R) layer of phellum cells.

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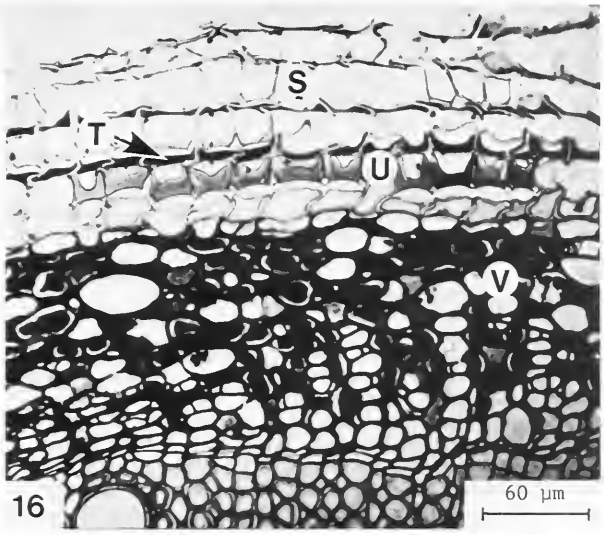

FIG. 16.
Transverse section of the stem of *E. zuluensis*. Note the absence of thickened cell walls in the older phelloid layers (S) and presence in the younger layer (U). (T) phellem cell layer; (V) external phloem.

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S. Afr. Bot. 46 (1): 89–96 (1980)

A MICROAUTORADIOGRAPHIC STUDY OF THE TRANSLOCATION OF ^{14}C-LABELLED ASSIMILATES IN *ERAGROSTIS CURVULA* (SCHRAD.) NEES

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Abstract

Microautoradiography was used to determine the cellular distribution of translocated ^{14}C-labelled assimilates in *Eragrostis curvula*. The assimilates were labelled by allowing a single leaf to photosynthesize in an atmosphere containing radioactive carbon-dioxide. It was found that the phloem was the main tissue involved in translocation; there was radial translocation from the phloem to other tissues; and some ^{14}C was transported, apparently in the gaseous form, through the lysigenous cavities of vascular bundles.

Uittreksel

'N MIKRO-OUTORADIOGRAFIESE STUDIE VAN DIE TRANSLOKASIE VAN ^{14}C-GEMERKTE ASSIMILATE IN *ERAGROSTIS CURVULA* (SCHRAD.) NEES

Mikro-outoradiografie is gebruik om die sellulêre verspreiding van getranslokeerde ^{14}C-gemerkte assimilate in *Eragrostis curvula* te bepaal. Die assimilate is gemerk deur 'n enkele blaar toe te laat om te fotosintetiseer in 'n atmosfeer wat radioaktiewe koolstofdioksied ($^{14}CO_2$) bevat. Dit is bevind dat die translokasie hoofsaaklik in die floëem plaasgevind het; daar was radiale translokasie van die floëem na die ander weefsels; van die ^{14}C is blykbaar in 'n gastoestand deur die lisigene holtes van die vaatbondels vervoer.

Introduction

The distribution patterns of translocated ^{14}C-labelled photosynthate in grasses have been investigated mainly by gross or "whole plant" autoradiographic methods, eg. Williams, 1964; Sagar and Marshall, 1966; Marshall, 1967; Barnabas and Steinke, 1975; and others. There is little information, however, about the distribution of translocated photosynthate within the tissues of these plants. The aim of the present study was to investigate the distribution of translocated ^{14}C-labelled photosynthate at the cellular level in *Eragrostis curvula* by micro-autoradiographic techniques. Since a large proportion of photosynthate is water soluble, techniques to prevent leaching of these soluble compounds prior to and during microautoradiography were used.

Material and Methods

Seeds of *Eragrostis curvula* (cultivar Ermelo) were germinated in moist sand. When the seedlings reached the two-tiller stage they were transferred to 1 ℓ bottles

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covered with aluminium foil. The bottles contained a modified Hoagland nutrient solution. The plants remained in a glasshouse under conditions similar to those reported earlier (Barnabas and Steinke, 1975). Plants at the early flowering stage (before anthesis) were used in this study.

The method of introducing ^{14}C into the plants was similar to that described previously (Barnabas and Steinke, 1975). One hundred microcuries of $^{14}CO_2$, generated from $Na_2{}^{14}CO_3$ (specific activity 55 mc/mm), were offered to the third leaf on the culm for 20 min. After a further 30 min photosynthesis in unlabelled CO_2, the plants were harvested.

Samples for microautoradiography were taken from four different parts of the plant (see Fig. 1), namely, from the lower part of the treated leaf (TL) which was not enclosed in the assimilation chamber; from the internode below the node of insertion of the treated leaf; and from two parts of the internode above the node of insertion of the treated leaf. Samples, not exceeding 2 mm in thickness, were taken from each part and were frozen immediately in a mixture of isopentane and dry ice.

A simple, high vacuum freeze-drying apparatus similar to that described by Jensen (1962), was used to freeze-dry the samples. During freeze-drying, the samples were kept frozen by immersing the dehydration chamber in a mixture of dry ice and 65 % ethanol.

Freeze-drying was allowed to continue until the material appeared whitish in colour (ca. 96 h). According to Jensen (1962) the whitish colour of the samples is an indication that the dehydration process is complete. The samples were then infiltrated with paraffin wax under vacuum according to the procedure given by Glick and Malstrom (1952). However, during paraffin wax infiltration only about one third of the samples sank. Those that did not sink were left in molten wax in an oven. After a week about half of these sank. Those that did not sink were discarded. Samples were embedded in fresh filtered paraffin wax according to standard embedding procedures and transverse sections (10 μm thick) were cut on a sledge microtome.

Autoradiographic plates were prepared by wet-mounting pieces of Kodak AR.10 stripping film, with the emulsion side upward on subbed glass slides, i.e. slides coated with a thin layer of gelatin. Mounting of sections on to autoradiographic plates and processing of the plates after exposure were based on methods modified from Haasbroek, Noggle and Fleming (1962). The autoradiographic plates were developed in Kodak D–19b developer and fixed in Kodak acid fixer. Well-preserved sections, superimposed upon their developed images were mounted in a medium having a refractive index of 1,525. Coverslips were applied and the microautoradiographs examined by bright-field microscopy and photographed.

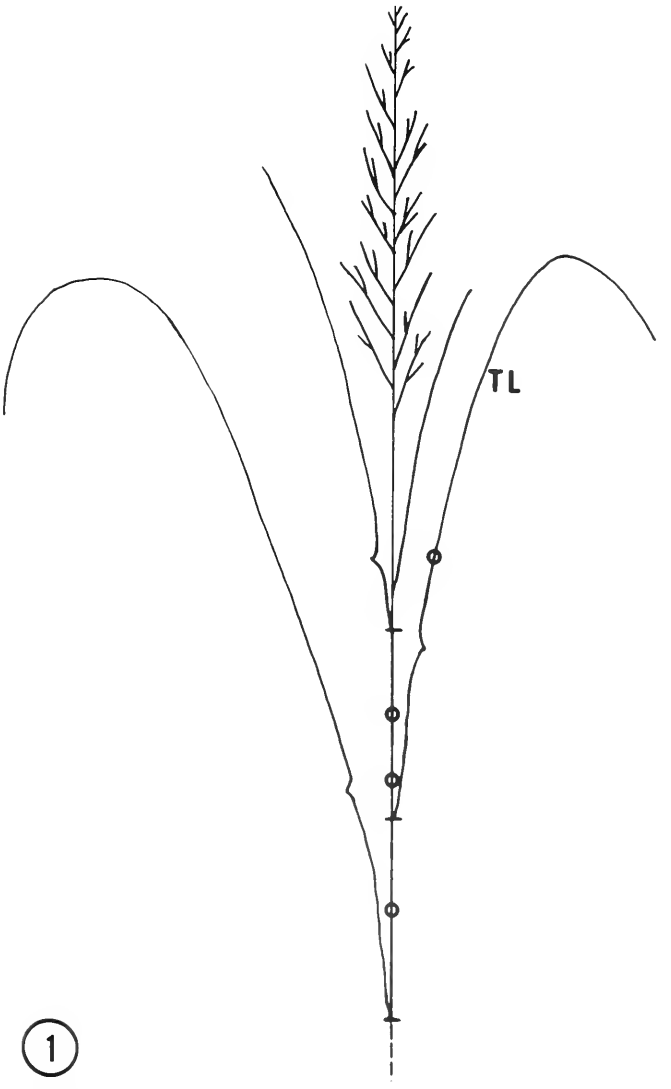


FIG. 1

Diagrammatic representation of part of a plant of *Eragrostis curvula*. Circles indicate portions from which samples were taken for microautoradiography. TL, treated leaf.

Results

The distribution of ^{14}C-labelled assimilates within the tissues of samples taken from four different parts of the plant is shown in Figs 2–5. These microautoradiographs are representative of many microautoradiographs obtained.

Figure 2 shows the distribution of radioactivity in a portion of a vascular bundle of the treated leaf. Although there was too much radioactivity in this section for good resolution, it can clearly be seen that ^{14}C is localized in the phloem. Radioactivity is heavily concentrated in two phloem elements, with smaller amounts in other phloem elements as well.

Figure 3 reveals the presence of radioactivity in parenchyma cells of a section of the internode below the node of insertion of the treated leaf. The resolution of this microautoradiograph is better. Although radioactivity is fairly evenly distributed, a clumping of silver grains is seen in parts of many cells. Labelled assimilates were also detected in the phloem of a vascular bundle near these parenchyma cells.

In Figure 4 the distribution of radioactivity in a vascular bundle and the surrounding tissues of a section of the internode above the node of insertion of the treated leaf, is shown.

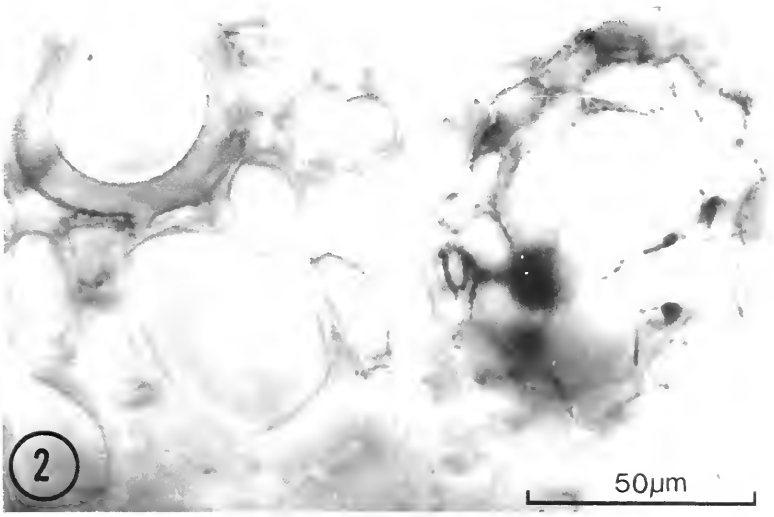
Figure 5 shows ^{14}C concentrated mainly around the lysigenous cavity area of the xylem. This section was taken from the middle of the internode above the treated leaf.

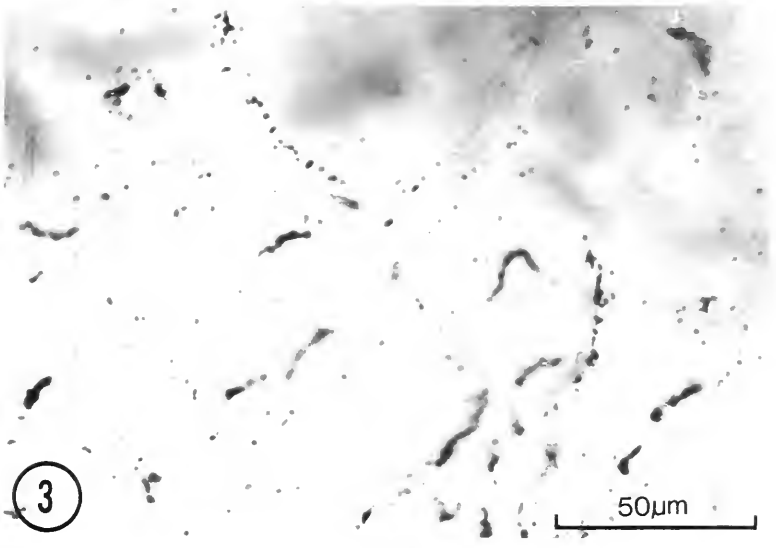
Discussion

Since no radioactivity was present in the xylem of the treated leaf, ^{14}C-labelled photosynthate was translocated from the treated leaf through the phloem. In a detailed investigation of the nature of the substances translocated in *E. curvula* (unpublished work) sucrose was found to be the principal compound exported from the treated leaf. Therefore the radioactivity in the phloem elements was probably due to ^{14}C-sucrose. It is interesting to note that not all phloem elements were involved in translocation during the time of the experiment. This finding is in agreement with that obtained by Trip and Gorham (1967) in squash. In contrast Geiger, Saunders and Cataldo (1969) observed that nearly all sieve tube elements in sugar beet petioles translocated ^{14}C-labelled assimilates.

The presence of radioactive material in parenchyma cells of the internode below the treated leaf showed that radial translocation had probably occurred. Radial translocation was probably also responsible for the presence of labelled material around the tissues of a vascular bundle from a section of the internode above the treated leaf. Such movement could have occurred, since a period of 50 min elapsed from exposure to $^{14}CO_2$ till harvest.

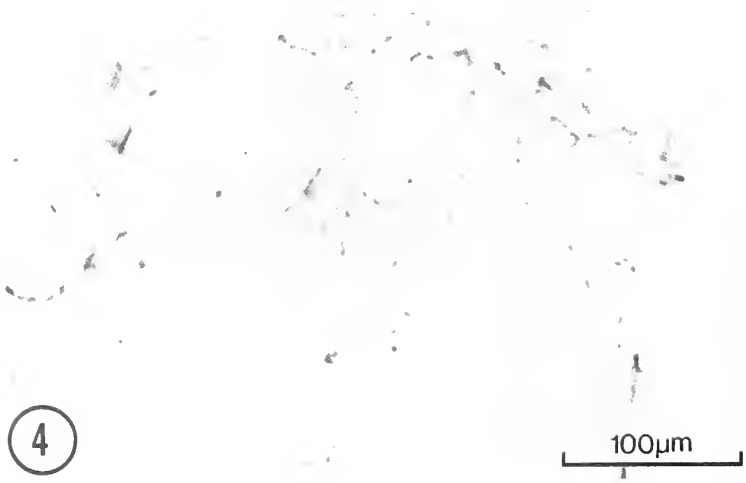
In both these microautoradiographs (Figs 3 and 4) a clumping of silver grains was observed in parts of many cells. Trip and Gorham (1967) also noted clumps of silver grains in radial sections showing the distribution of radioactivity in sieve

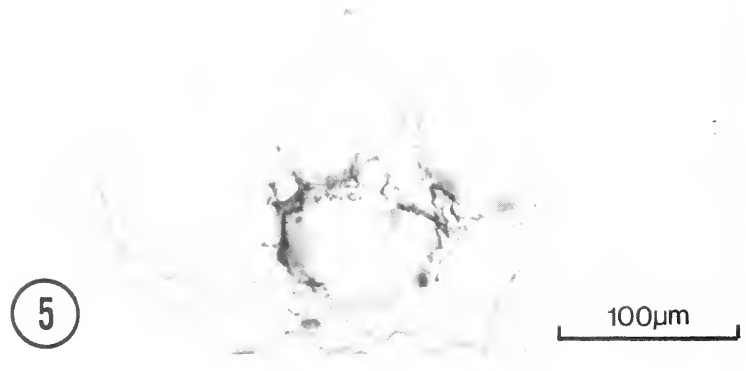




FIGS 2–3

Microautoradiographs of transverse sections. 2. The treated leaf showing ^{14}C localized in the phloem of a vascular bundle. 3. ^{14}C is localized in parenchyma cells of the internode below the treated leaf.





FIGS 4–5

Microautoradiographs of transverse sections. 4. The internode above the treated leaf showing the distribution of ^{14}C within and around a vascular bundle. 5. ^{14}C is localized around the lysigenous cavity of a vascular bundle in the middle of the internode above the treated leaf.

tube elements of squash. The authors suggested that this clumping may be due to the irregular displacement of the cytoplasm during the freezing and embedding procedures. Such a phenomenon may have occurred in this study as well.

The localization of radioactivity mainly around the lysigenous cavity in sections taken from the middle of the internode above the treated leaf could be an artifact of preparation, but is more probably due to the gaseous movement of $^{14}CO_2$ through the lysigenous cavity. Lysigenous cavities, found in many members of the Gramineae, are defined by Metcalf (1960), as longitudinal air canals formed by the breakdown of protoxylem vessels. It is possible that some $^{14}CO_2$, while in transit through a lysigenous cavity, could have gone into solution on contact with the wet walls of the cells surrounding this cavity.

Long distance gaseous movement through intercellular air spaces has been demonstrated by Barber, Ebert and Evans (1962) and by Yoshida and Broadbent (1975). The former investigators showed that air labelled with ^{15}O moved from the shoot to the root in rice and barley plants by gaseous diffusion through continuous intercellular air spaces. Yashida and Broadbent (1975) showed that ^{15}N-labelled nitrogen gas also moved from the shoot to the root in rice plants. The movement of $^{14}CO_2$ in intercellular air spaces was demonstrated by Penny and Nelson (1970) in leaves of soyabean and *Pelargonium*. These investigators showed by whole leaf autoradiography that ^{14}C, applied to localized areas of the leaves, first moved through the intercellular air spaces of the mesophyll as $^{14}CO_2$ before being fixed in photosynthesis. These authors also suggested that the generation of $^{14}CO_2$ in the assimilation chamber around the treated leaf, would favour gaseous movement through the air spaces since there would be a slight increase in pressure and a concentration gradient would also be established. The latter conditions existed in the present investigation when the treated leaf assimilated $^{14}CO_2$.

This study has shown that the movement of $^{14}CO_2$ through air space systems, during translocation experiments, may be possible and further investigation in this direction is needed.

Acknowledgement

This work formed part of a study of the translocation of ^{14}C-labelled assimilates in *E. curvula* for an M.Sc. degree. Financial assistance from the Council for Scientific and Industrial Research is gratefully acknowledged.

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Book Review

FLORA ZAMBESIACA. Volume Four, edited by E. Launert, with pp. 658 + 168 line drawings, 1 colour frontispiece. Families covered: Rosaceae—Cornaceae (Crassulaceae excepted). London: Flora Zambesiaca Managing Committee, 1978. Price £20.00.

The publication of another volume of *Flora Zambesiaca* is an event of importance to those who study the plants of Africa south of the Sahara and to all who have interest in these plants.

Volume Four, as the Editor's Preface states, is the first of the sequence to be published in its entirety instead of in two or more parts. The large number of pages makes for less easy handling than with the previous numbers, but the pages mostly lie flat for working so the thickness may not prove a disadvantage. Again the well executed line drawings of representative plants are a pleasure to the eye and a help to the user, while the text, as before, seems to have been meticulously proof read.

Thirty four families are dealt with. A number are small taxa comprising, at least in the area under consideration, only few genera and species: examples are Vahliaceae—D. M. Bridson, Montiniaceae—E. J. Mendes, Brexiaceae—N. K. B. Robson, Myrothamnaceae—E. J. Mendes, Oliniaceae—B. Verdcourt, Sonneratiaceae—A. Fernandes, Trapaceae—J. P. M. Brenan. Despite limited size these taxa are not necessarily straightforward taxonomically. Variability has frequently been remarked upon by the specialist authors who have also drawn attention to alternative taxonomic treatments where these exist, and to plants or features of plants that require further study.

Other families are very much larger and already "famous" for the problems they present. Thus the accounts of Combretaceae—A. W. Exell, Myrtaceae—F. White, Passifloraceae—R. and A. Fernandes, Cucurbitaceae—C. Jeffrey and Umbelliferae and Araliaceae—J. F. M. Cannon are likely to prove valuable not only to herbarium personnel, but to ecologists and others who require identifications of plants in the course of their work. Also deserving special mention, but in a slightly different context since the plants are less often woody or climbing and thus perhaps less significant in the overall vegetation, but often problematical when naming is required, are the accounts of Aizoaceae sensu lato (here split into Molluginaceae, Aizoaceae sensu stricto, Mesembryanthemaceae and Tetragoniaceae—M. L. Gonçalves) and Lythraceae—A. Fernandes. To assist with problems relating to the delimitation of taxa in *Syzygium*, a sheet giving the outline shapes and relative size ranges of leaves of species and interspecific hybrids is tucked into a pocket on the back cover.

Crassulaceae, which should have been included, had unfortunately to be omitted due to the death of the world authority on this taxon, Dr Raymond-Hamet. The account of this family, now to be written by Dr Rosette Fernandes, will be published out of sequence in the next volume or part of the Flora to appear. In view of this omission it is unfortunate (although well understandable in the circumstances) that the frontispiece, the only colour plate in the volume, depicts *Kalanchoe rotundifolia*.

Many of the families covered in Volume Four have already been dealt with for the *Flora of Tropical East Africa*, sometimes by the same specialist, sometimes by another, so that it is felt that the tropical representatives are now reasonably well documented. However some taxa extend further south. Only few of the families dealt with in Volume Four have been included in the volumes of the *Flora of Southern Africa* published so far. Much remains to be done in the southern part of Africa. Most of us are well aware of this and of the need for speed before vegetational changes are too extreme.

In the Volume under review nine new names and taxa are published. Two of these (both in *Begonia*) are species newly described; six are new combinations of names; one is a change in status. It is perhaps interesting to note that in this volume "Umbelliferae" is used without reference to the less familiar alternative "Apiaceae".

As is usual with regional floras, a brief summary of the distribution of a taxon outside the area of the Flora follows the citation of specimens. Since this review is for a South African journal it might be as well to stress that the distributions given for the Republic and its associated countries are approximations. For example: both *Ceriops tagal* and *Rhizophora mucronata* are stated to extend "to S. Africa (Durban)" whereas, to the best of my knowledge, the former falls away at Kosi Bay while the limit for the latter is slightly south of Durban; *Pteleopsis* is not recorded for S. Africa but occurs in Tongaland; *Gunnera perpensa* is not recorded for Natal where it is widespread along streambanks.

At twenty pounds the cost of the volume is by no means excessive considering the information it contains.

K. D. Gordon-Gray.

Jl S. Afr. Bot. 46 (2): 99–107 (1980)

THE SEASONAL VARIATION OF THE PHENOLIC DILACTONE LEUCODRIN IN *LEUCADENDRON ARGENTEUM* R. Br.

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Abstract

The seasonal variation of the occurrence of leucodrin in *L. argenteum* was followed for 15 months; samples consisting of 10 g twigs were collected for testing every three weeks. The leucodrin was extracted from the plant material and partially purified before the concentration of its TMS ether was determined by GLC. The results show that the leucodrin content of the leaves increased as the new leaves of the terminal bud increased in size. This increase was from approximately 9 mg to 15 mg/g fresh weight. After the leaves were fully developed the leucodrin concentration decreased until the next season when new leaves started to develop from the terminal bud. This same pattern has been reported for other phenolic compounds from different plant sources. The moisture content of *L. argenteum* leaves also showed a seasonal variation; the maximum moisture content was found during the wet summer with minimum moisture content being found during the dry winter when there was no rain for several months.

Uittreksel

DIE SEISOENSVERANDERING VAN DIE FENOLIESE DILAKTOON LEUCODRIN IN *LEUCADENDRON ARGENTEUM* R. Br.

Die seisoensverandering van die voorkoms van leucodrin in *L. argenteum* was vir 15 maande gereeld ondersoek; monsters van ongeveer 10 g stingels was elke drie weke versamel en dan getoets. Die leucodrin was uit die plant materiaal ge-ekstraheer en gedeeltelik gesuiwer voordat sy eter bepaal is deur gaschromatografie. Die resultate bewys dat die leucodrininhoud van die blare algaande vermeerder soos die nuwe blare van die terminale bloeisel groter word. Hierdie vermeerdering was van ongeveer 9 mg tot 15 mg per g vars gewig. Nadat die blare ten volle ontwikkel was het die leucodrinkonsentrasie verminder tot die volgende seisoen wanneer die blare weer begin ontwikkel het vanaf die terminale bloeisel. Dieselfde patroon was gerapporteer vir ander fenoliese stowwe van verskillende ander plantbronne. Die voggehalte van *L. argenteum* blare het ook 'n seisoensvariasie getoon; die maksimum voggehalte is gevind gedurende die nat somer en die minimum voggehalte gedurende die droë winter wanneer daar geen reën was vir 'n hele paar maande nie.

Introduction

Leucodrin has been known to occur in various *Leucadendron* spp. since 1886 and the structure of this phenolic dilactone has now been fully established (Perold and Pachler, 1966). Its distribution includes the genus *Leucadendron* and several *Leucospermum* spp. (both in the Proteaceae) and it has been found in varying amounts in the different species examined. Murray (1962) reported 15% and

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Murray and Bradshaw (1966) reported up to 20% leucodrin in the leaves of *Leucadendron salignum* while Plouvier (1964) reported 2,3% in the influorescences of *Leucospermum reflexum* and 1,1% in its leaves. He also found similar results for *Leucadendron argenteum*.

It has been suggested that leucodrin could act as a carbohydrate storage product (Hegnauer, 1969). He based this decision on the large amounts of the compound present and its relationship to sugar. One way of incorporating the sugar may involve a Michael-type condensation of *p*-coumaric acid and L-γ-galactonolactone (Diamand and Rogers, 1964; Perold, Hodgkinson, Howard and Kruger, 1972). Another possible biosynthetic route could involve the reductive C-C coupling of *p*-coumaric acid and ascorbic acid (Couchman *et al.*, 1973). Whichever way leucodrin is biosynthesized, one molecule of carbohydrate is combined with one molecule of *p*-coumaric acid which itself is formed from the carbohydrate pool via the shikimic acid pathway.

Since equal amounts of phenolic and sugar are involved in this unusual compound it was decided to attempt to determine which way leucodrin was behaving: as a phenolic or as a carbohydrate. One way to solve the problem was to study its variation in concentration during seasonal change. The literature reports seasonal changes for a wide variety of plant constituents and the results of this study could then be compared with these reports.

Over the past few years much has been published about biological rhythms; there are many variations in the type of rhythm, perhaps the best known being the 24 hour or circadian period. Some work has been published on annual variation in organisms and it has been found that for the various metabolic pools and functions, maxima usually occur mid-summer with the minima occurring in the winter. Studies using beans show that O_2 consumption and water uptake followed the same well-defined pattern of maximum rate in summer and minimum in winter. Similar studies on O_2 consumption in potatoes showed the same pattern (Palmer, 1976). Also, the plant to be sampled in these experiments was growing in a summer rainfall area and it was decided to monitor its leaf moisture content. It could be of interest to see if the leaf moisture content follows the pattern of rainfall, i.e., very high rainfall in the summer with no rain for several months during the winter.

Material and Methods

All plant material was collected from one tree which was located near Jan Smuts House, University of the Witwatersrand, Johannesburg. Samples were collected at the same time of day every 3 weeks for 15 months, starting in February, 1977. The moisture determinations were done in triplicate by drying the samples in an oven at 120° for 20 hours. Samples, taken for both moisture and leucodrin determinations, were the tips of branches and weighed approximately 10 g.

The leucodrin content was determined by GLC and the samples were prepared in the following manner. The sample of fresh plant material taken for the leucodrin determinations was ground in MeOH in a Waring Blendor and then exhaustively extracted in a Soxhlet extractor. This extract was partially purified by column chromatography on silica gel using benzene:ethyl acetate:methanol (5:3:2 v/v). The fractions containing leucodrin were collected and made to a 10% solution in MeOH, and 0,1 mℓ of this was taken for determination by GLC. All determinations were done in duplicate with standard leucodrin solutions of known concentrations run as references. All samples were taken to dryness in small tubes which were then sealed with septa prior to silylation. The trimethylsilylethers of the samples were formed by silylation using 50 $\mu\ell$ of a stock solution which comprised 10 mℓ dry pyridine, 1 mℓ trimethylsilylchloride, and 2 mℓ hexamethyldisilazane. After heating at 90° for 1 hour, 1 $\mu\ell$ of the silylated sample was injected into a Pye series 105 GLC apparatus. The column was 10% Si 52 on Anakrom and had dimensions of 0,004 × 2,0 m. All samples were run isothermally at 300 °C.

The leucodrin content was determined only on a fresh weight basis and the data in Figure 1 for the leucodrin content based on dry weight was calculated using the moisture content.

Results and Discussion

The leucodrin content of *L. argenteum* as it varies with seasons is presented in Figure 1; the leucodrin content is presented on both a dry weight basis and a fresh weight basis. This is done to allow for any variation in moisture content which also shows a seasonal variation. Figure 1 shows that this seasonal variation in moisture affects the pattern of leucodrin content. On a fresh weight basis the maximum leucodrin content appears to maintain a plateau from July until November which covers the end of winter through spring until the beginning of summer. When the leucodrin content is calculated on a dry weight basis it follows a pattern having a maximum during the period of leaf expansion in late winter and early summer and declining during late summer which is the period of negligible growth.

Figure 2 reports the seasonal variation of leaf moisture content along with the actual rainfall recorded at Joubert Park, Johannesburg; this weather station is approximately 1 km from the point where the plant material was collected. From this figure it can be seen that the maximum moisture content of the leaves of *L. argenteum* was found during the rainfall season, summer, and the minimum leaf moisture content occurred during the winter when there was no rain at all for several months.

It is probable that Plouvier (1964) found leucodrin present in *Leucodendron argenteum* but not in *Leucospermum reflexum* as he reported. The compound found in the latter species was probably the diastereoisomer, conocarpin, or one

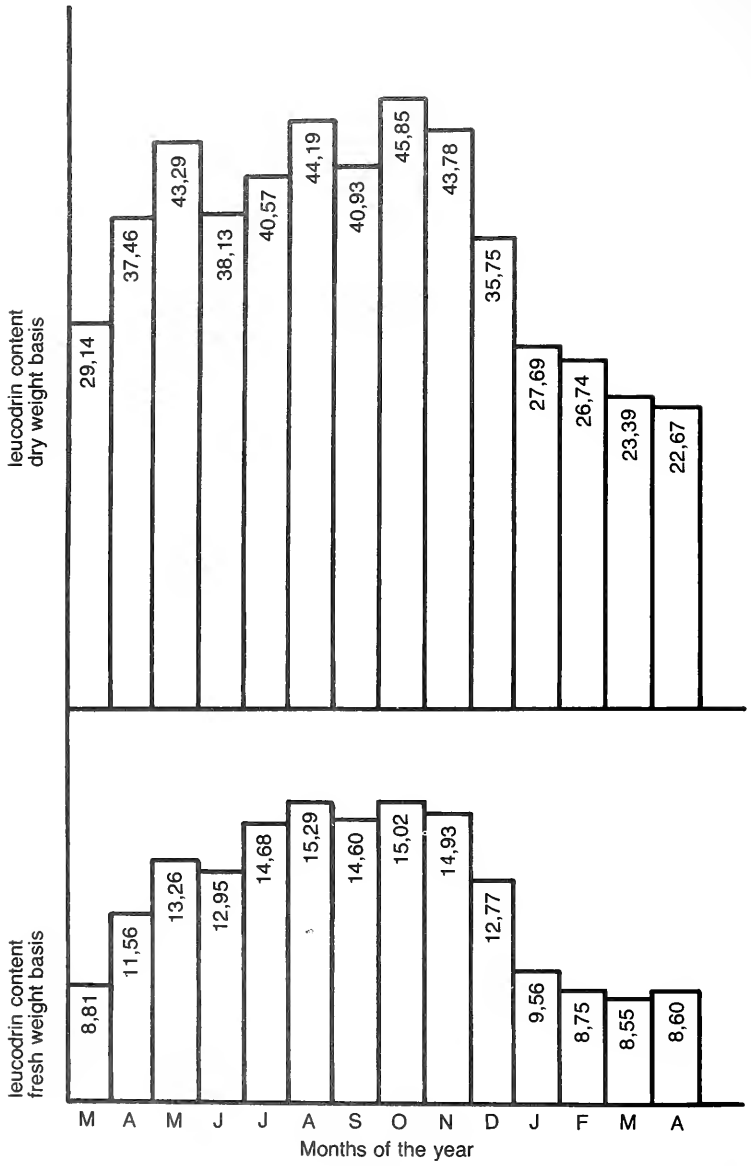

FIG. 1.
Leucodrin content of *Leucodendron argenteum* leaves in mg/g dry weight and mg/g fresh weight.

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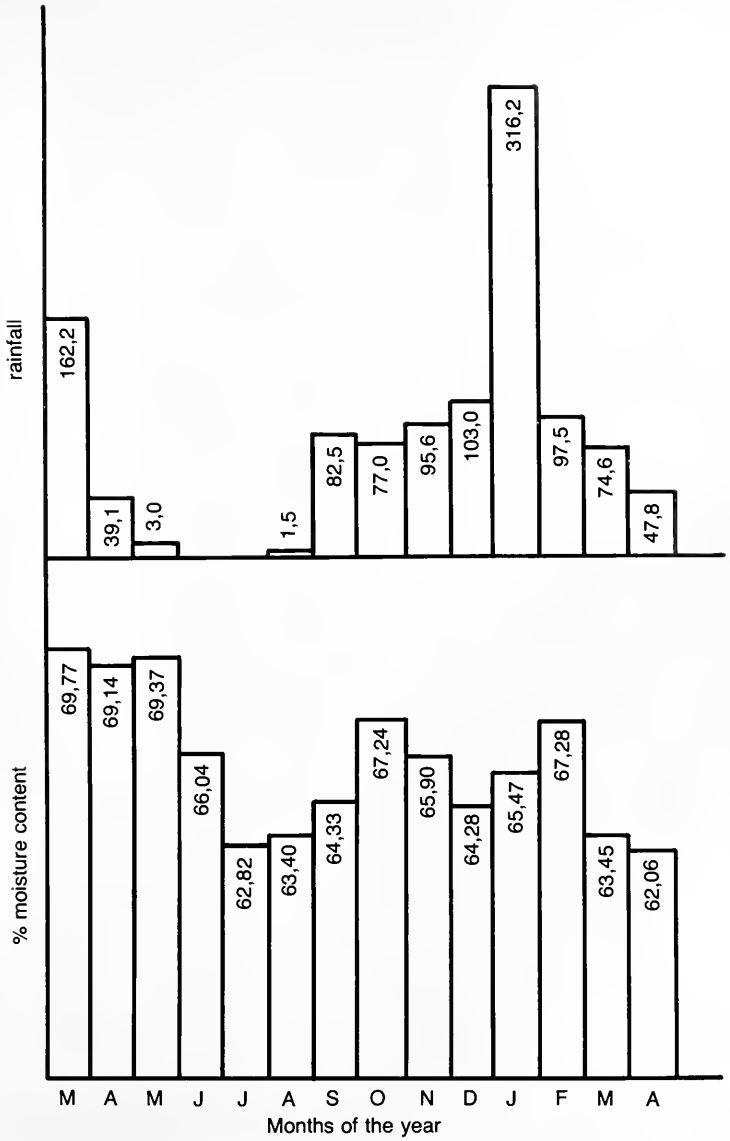

FIG. 2.
Leaf moisture content of *Leucadendron argenteum* and the rainfall amount (mm) for the same fourteen month period.

of its related compounds: reflexin or conocarpic acid (Kruger and Perold, 1970; Perold, Hodgkinson and Howard, 1972). It has been found that all *Leucadendron* spp. and a few *Leucospermum* spp. examined contained leucodrin while the majority of *Leucospermum* examined contained the diastereoisomer, conocarpin.

During this study *Leucadendron salignum* was used as a source of leucodrin for one quantitative determination. The reason only one determination was carried out was due to the local scarcity of plant material of this species and its relatively small leaf size. It was found that *L. salignum* leaf material yielded 5,40% leucodrin on a fresh weight basis and 11,25% on a dry weight basis. This is in comparison with the findings of Murray and Bradshaw (1966) who reported up to 20% leucodrin for this species.

Some work has been reported on the changes in plant hormone concentrations in leaf material during the growing season. Van Staden (1976, 1977) found that in both *Ginko biloba* and *Salix babylonica*, the cytokinin activity was related to leaf maturity. In young, immature leaves the cytokinin activity was extremely low but this increased as the leaves matured. In terms of season the lowest cytokinin content was found during October and the highest content was in summer through autumn (December until June). Another study on the changes in cytokinin content was carried out on *Populus* X *robusta* (Hewett and Wareing, 1973). This study showed that cytokinin activity was at a maximum in expanding leaves, and falling off as the leaves aged. This gave the highest concentrations of cytokinins in mid-summer.

The trees used in these above studies were deciduous while *L. argenteum* is an evergreen broad-leafed tree. Like the cytokinins, leucodrin increased during leaf development but it is probable that *L. argenteum* produces its leaves earlier in the season than those used in the cytokinin activity studies and hence the maxima and minima for concentration do not coincide.

Fry and Phillips (1977), in their study on photosynthesis in conifers in relation to annual growth cycles, found a similar pattern to leucodrin production. Using this evergreen species they found that photosynthetic efficiency of new needles showed an overall decline from just after needle maturity until just before bud-break in the next season. After bud-break the photosynthetic rate increased parallel with needle development until the previous maximum was reached with leaf maturity falling off to a minimum before the terminal bud breaks is very similar to the leucodrin concentration in *L. argenteum*.

To assess the carbohydrate production pattern of plants, sugar cane was taken as an example. Production of sugar was lowest at temperatures below 21 °C, and highest along with maximum growth rate, during the hot, sunny days of summer (above 32°) (Bass *et al.*, 1957). The pattern of leucodrin accumulation in *L. argenteum* certainly is not similar to that of sugar in sugar cane. Comparing Figure 1 and Figure 3 it can be seen that during the hottest days of summer (October to March) the leucodrin content is decreasing instead of increasing as sugar does.

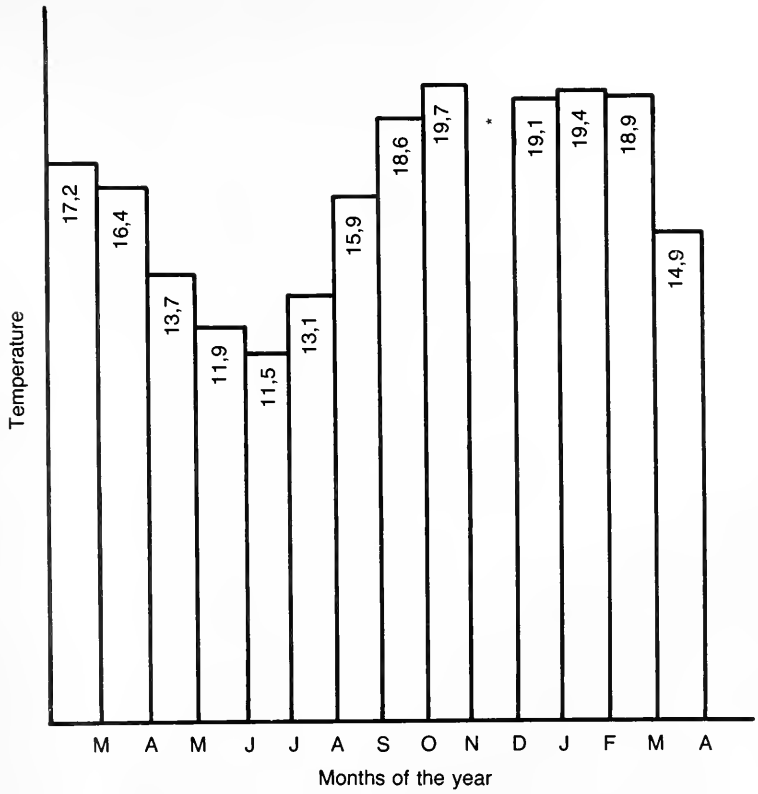

FIG. 3.
Mean monthly temperatures (°C) at Joubert Park, Johannesburg for the experimental period.
*Data not available.

Phenolic compounds exhibit a wide variation in concentration due to season. A linear increase in the amount of shikimic acid was found with the increase in weight of the leaves of *Eucalyptus sieberiana* (Hillis, 1958). The maximum amount of shikimic acid was present in the leaves which had just reached maximum size. After this the shikimic acid content of fully developed leaves decreased with the age of the leaf. Hillis and Swain (1959) found a very similar pattern in *Prunus domestica*. They analysed leaf material for total phenols, leucoanthocyanidins and flavonols, at intervals during the growing season. The results showed that the amounts of these compounds increased with increasing leaf

size until the leaves reached maximum size and then the content of phenols decreased as the leaves aged.

The concentration pattern of the phenolic dilactone leucodrin follows very closely the concentration patterns of shikimic acid or total phenols. In *L. argenteum* the terminal bud is formed at the end of one season but due to the mild winter it does not lie dormant during the winter but rather maintains a slow growth pattern maturing in the early summer. It is this same pattern that the leucodrin concentration follows, reaching a maximum in the newly developed mature leaves, and decreasing as the fully developed leaves age until the next season's terminal bud starts developing. Since shikimic acid is a precursor of *p*-coumaric acid which, in turn, is probably a precursor of leucodrin, then the leucodrin content should follow the same pattern as the shikimic acid content.

Why does leucodrin accumulate to such a large extent in the leaves of *Leucadendron* spp.? Since its seasonal variation in concentration closely follows the seasonal pattern of a phenolic compound and not a carbohydrate, it is probably functioning as a phenolic type compound and not, as Hegnauer suggested, a carbohydrate. Since many phenolic compounds are phytotoxic, leucodrin formation could simply be one method of detoxifying *p*-coumaric acid. It has been shown that some plants detoxify hydroxylated cinnamic acids by forming glucose esters (Asen and Emsweller, 1962; Glennie and Bohm, 1966). This addition of a sugar onto the phenolic compound could also aid the plant in translocating the compound or make it easier for transport across membranes, e.g., transporting it into the vacuole for storage.

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NOTES ON *TULBAGHIA*: 2

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(Botany School, Oxford, England)

Abstract

A. *Tulbaghia violacea* Harv. is the legitimate name for *T. cepacea* L.f. Its taxonomic status is discussed.
B. The correct name for *Tulbaghia fragrans* Verdoorn is *Tulbaghia simmleri* Beauv.
C. Two new localities for *Tulbaghia verdoornia* Vosa & Burbidge have been found within 40 km of the site of collection of the type specimen.

Uittreksel

NOTAS OOR *TULBAGHIA*: 2

A. *Tulbaghia violacea* Harv. is die wettige naam vir *T. cepacea* L.f. Sy taksonomiese status word bespreek.
B. Die korrekte naam vir *Tulbaghia fragrans* Verdoorn is *Tulbaghia simmleri* Beauv.
C. Twee nuwe vindplekke vir *Tulbaghia verdoornia* Vosa & Burbidge is binne 40 km van die plek waar die tipe-eksemplaar versamel is, gevind.

A. On the Legitimacy of *Tulbaghia cepacea* L.f.

In my previous account on the taxonomy of the genus *Tulbaghia* (Vosa, 1975), I considered that the rules of nomenclature should only be applied after the taxonomic facts had been established.

In accordance with my views at the time, Linn. fil. could not reasonably be regarded as having included *T. capensis* L. into the circumscription of his new species, *T. cepacea*, and I upheld this latter name as legitimate. However, later studies and references to similar problems in other taxa and the opinions of my learned colleagues, have shown the difficulties of assessing the importance and meaning of such early presentations. In this case it is difficult to understand Linn. fil.'s decision of reducing *T. capensis* L. to a synonym of his new species, a decision which might be thought disrespectful to his father. He might have considered the name *capensis* inappropriate since both his new species, *alliacea* and *cepacea* also come from the Cape. It is also possible that he did not examine the specimens involved and that he relied on Linnaeus's description which, in its broadest sense, can include both *capensis* and *cepacea*.

Whatever the explanation, I have come to the conclusion that, in conformity with the current rules of nomenclature, *Tulbaghia cepacea* L.f. must be regarded as a superfluous name.

Therefore, I propose to consider *Tulbaghia violacea* Harv., already treated as a

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synonym of *T. cepacea* L.f. (Vosa, 1975), as the correct name for this latter entity.

Field studies have shown that because of the extreme variability of the taxon in question throughout its range, between and within single populations, use of the size as a character, to divide the species into separate varieties (Burbidge, 1978) is unreliable.

The typification of *Tulbaghia violacea* Harv. is as follows:

Tulbaghia violacea Harvey in Bot. Mag. **64:** t.3555 (1837). Typification: Described and illustrated from cultivated material in the Ludwigsburg Garden, Cape Town by Harvey, t.3555, iconotype. *T. cepacea* L.f., Suppl. Pl. 194 (1781), *quoad descr. excl. syn., nom. illeg.*

Icon.: Harvey l.c.; Vosa in Annali Bot. (Roma) **34:** 113–117, fig. 22 and 23; pl. XX, figs. 3, 4 and 5 (1975), incl. var. (as *T. cepacea* L.f.).

B. *Tulbaghia simmleri* Beauv., the Correct Name for *Tulbaghia fragrans* Verdoorn

In my cytotaxonomic revision of the genus *Tulbaghia* (Vosa, 1975) I mentioned the absence of herbarium specimens of *T. simmleri* Beauv. Later research and enquiries have shown that this is not the case. The type material of *T. simmleri*, together with the drawings and sketches used for the general description, exist and are kept in the Herbarium of the Conservatoire et Jardin Botanique of the University of Geneva (G) at Chambesy (Switzerland). The material, consisting of two sheets and drawings, have been lent to me through the courtesy of the Director, Prof. Dr J. Miège and are illustrated in Figs 1 and 2.

The plant described by G. Beauverd, in Bull. Herb. Boissier **8:** 988 (1908), was part of a parcel of bulbous plants sent to him by the Swiss missionary Henry A. Junod (see letter to Beauverd in Bull. Herb. Boissier **6:** 503, 1906) and cultivated by the gardener Simmler in the greenhouses at La Pierrière near Geneva. H. A. Junod was then stationed at the Evangelist Mission at Shilouvane, 25 km SE of Tzaneen (Northern Transvaal), which he established in 1899. He had a hut, which he called "Le Sanatorium", on the nearby mountain Mamotsuiri (Mamotseeri) where, with his family, he passed at least part of the hot summers away from the unhealthy low veld. There is no doubt that he collected *T. simmleri* on his way up the mountain or in the adjacent valleys. The locality is within the known range of *T. fragrans* and indeed I have collected plants of this species within 15 km of the Mission.

Careful study of the type specimens has led to the conclusion that *T. fragrans* and *T. simmleri* are in fact the same species. The only area of disagreement may be found in the large stigma, as shown in the Beauverd illustration. An analysis of several specimens, both as living plants and as exsiccata, from all over the range, has left no doubt about the identity of the species. It is likely that the large stigma owes its origin not to a mistake, as was suspected at the beginning of this study,

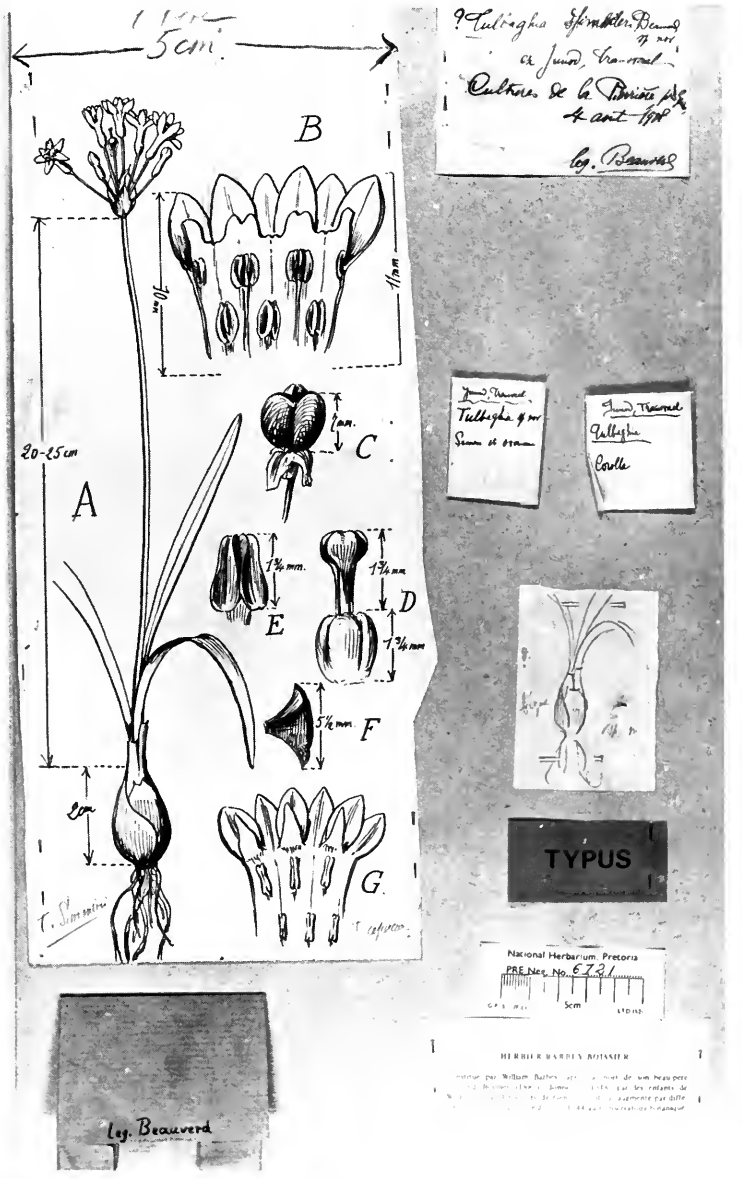

FIG. 1.
Sheet a. of the type specimens of *Tulbaghia simmleri* Beauv. Note the entire corona, with lobes about half its length in B, and the opened flower of *Tulbaghia violacea* Harv. (as *T. cepacea* L.f.) showing the three separate coronal lobes, drawn for comparison in G.

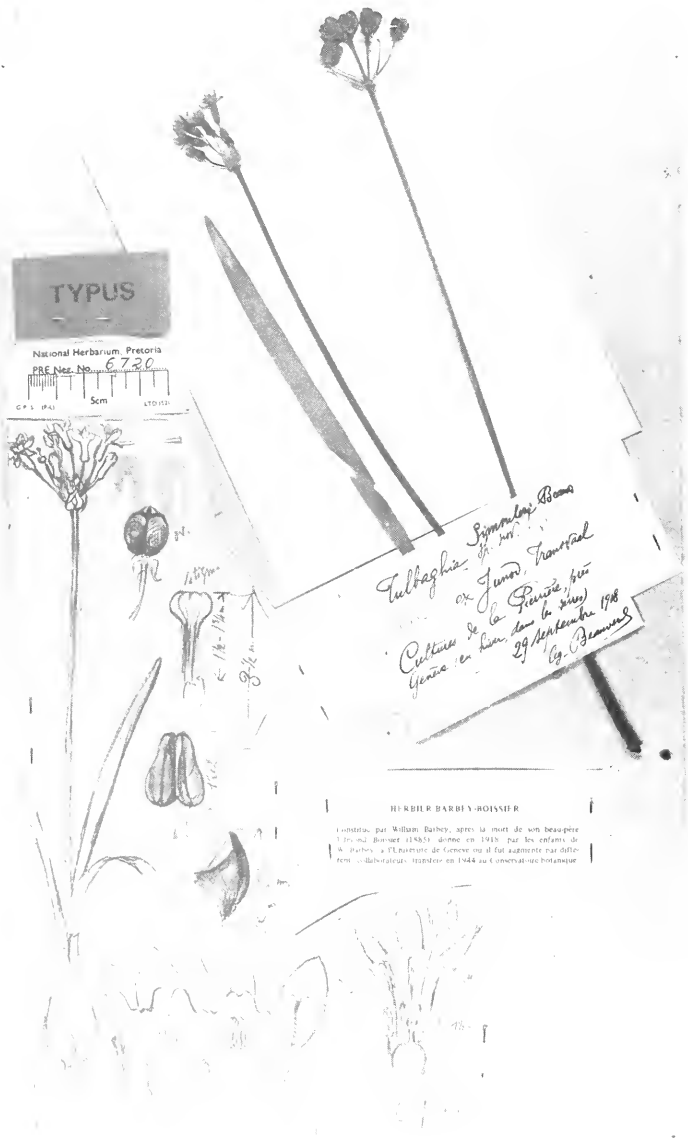

FIG. 2.
Sheet b. of the type specimens of *Tulbaghia simmleri* Beauv. The primary sketch for the published drawing, shown in Fig. 1, has been made on the reverse of a calendar leaf for Friday 20 July 1906.

but to the fact that the drawing for the dissected flower was made on dry or partially dry material. Experiments have shown that under such conditions the stigma, especially if pollinated, will appear much larger than in fresh or not pollinated material.

Burbidge (1978) believed *T. cepacea* L.f. (an illegitimate name) to be a synonym of *T. simmleri* Beauv. but this is incorrect.

The typification of *T. simmleri* Beauv. is as follows:

Tulbaghia simmleri Beauverd in Bull. Herb. Boissier **8:** 988 (1908). Type: Transvaal, Shilouvane, leg. H. A. Junod; ex hortus G; specimens and drawings on two sheets prepared by G. Beauverd (G, holo!).

Syn: *T. pulchella* Barnes, in S. Afr. Gard. **20**: 185 (1930); non Avé-Lall. (1844). Type: Eastern Transvaal, mountains near Pilgrim Rest, (2430-DD) *Knox-Davies* (NBG *731/29*, holo.).

T. daviesii C. H. Grey, Hardy Bulbs, **2**: 572 (1938), nom. nov. for *T. pulchella* Barnes.

T. fragrans Verdoorn, Fl. Pl. S. Afr. **11:** t.438 (1931). Type: Eastern Transvaal—(2430-DB): Dientje Farm, just N. of Bourke's Luck, *Celliers 8894* (PRE, holo.). Icon.: Beauverd (l.c.) Fig. 2 p. 988. Barnes (l.c.) Fig. A (as *T. pulchella*). C. H. Grey (l.c.) Fig. 3 (as *T. daviesii*). Verdoorn (l.c.) Fig. 438 (as *T. fragrans*). Vosa in Annali Bot. (Roma) **34:** 91, pl. XI, Fig. 3; 93, Fig. 13 (as *T. fragrans*).

Note: Tulbaghia simmleri sensu Burbidge (1978) = *T. violacea* Harv.

C. New Localities for *Tulbaghia verdoornia* Vosa & Burbidge.

Further distribution records for *T. verdoornia* Vosa & Burbidge are as follows:

CAPE—3228 (Butterworth): In a recently burnt vlei, near the railway at Mpuluswa, 15 km NE of Butterworth (-AA), *Vosa 1599* (OX), 7–10–77; on a tussocky, rocky hillside near the east side of the road from Idutywa, 60 km to Umtata (-AB), *Vosa 1601* (OX), 7–10–77.

These two collections are very important as they extend the range of the species. It was formerly known only as herbarium material collected in a single locality near Willowvale, between Mzolo School and Mendu, and as cultivated material without precise locality of collection. The two new localities are within 40 km of the site of collection of the type material.

Acknowledgements

I wish to thank Mr F. White, Curator of the Fielding—Druce Herbarium, Oxford, for reading the manuscript and for advice in the taxonomic treatment; Prof. Dr J. Miège, Director of the Conservatoire et Jardin Botanique of Geneva, Switzerland, for the loan of the type specimens of *Tulbaghia simmleri* Beauv.; Mr A. Charpin of the same Institute and Dr L. E. Codd of the Botanical Research Institute, Pretoria, for information about Henri Junod; Gordon and Margerite-Rose

McNeil of Ofcolaco, Transvaal, for the gift of valuable plant material and for kind hospitality; and the C.S.I.R. of South Africa for the award of a Fellowship.

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A NOTE ON THE SEED MORPHOLOGY OF THE GENUS *EUGENIA* L. (MYRTACEAE) IN SOUTHERN AFRICA

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ABSTRACT

The seed morphology of *Eugenia* L. in Southern Africa provides strong additional evidence in support of distinguishing between two species groups which were first recognised on the basis of anatomical characteristics. Descriptions are provided for each group of seeds.

These results could influence the taxonomic treatment of *Eugenia* L. occurring not only on the subcontinent, but throughout Africa.

UITTREKSEL

AANTEKENINGE OOR DIE SAADMORFOLOGIE VAN DIE GENUS *EUGENIA* L. (MYRTACEAE) IN SUIDER-AFRIKA

Die saadmorfologie van *Eugenia* L. in Suider-Afrika verskaf sterk, bykomende getuienis ter ondersteuning van 'n groepering van spesies in twee verskillende groepe wat aanvanklik op grond van anatomiese kenmerke voorgestel is. Beskrywings van die sade word vir elke groep verskaf.

Hierdie resultate kan die taksonomiese hersiening van *Eugenia* L. wat nie alleen in die sub-kontinent nie, maar ook in die res van Afrika voorkom, beïnvloed.

INTRODUCTION

A recent comparative anatomical investigation (Van Wyk, 1978; unpublished results) indicates that the *Eugenia* L. *sensu stricto* species of Southern Africa can be divided into two distinct groups based on certain anatomical characteristics (Van Wyk, Botha & Coetzee, 1980). Some of these characteristics enabled the author to distinguish between species which were confused in the past (Van Wyk, 1980). Consequently a critical study of the external morphology of the plants was undertaken in an attempt to find additional features which support the proposed grouping of the species.

In the present paper some preliminary results concerning the seed morphology are presented. The two species groups mentioned above will be referred to as Group X and Group Y.

In the taxonomy of the Myrtaceae, seed characteristics (especially embryonic structure) are of paramount importance in the delimitation of many genera and higher categories in the tribe Myrteae. The taxonomic value of the mature embryo was first recognised by De Candolle (1828) and today forms the basis of all the taxonomic treatments of this tribe (McVaugh, 1968).

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Despite the acknowledged taxonomic value of seed characteristics, it is often neglected in taxonomic work because of the lack of fruiting material in herbaria. The regional revisions of the genus *Eugenia* L. *sensu lato* for Malaya (Henderson, 1949) and Hawaii (Wilson, 1957) are probably two of the few works in which the nature of the seeds was described in some detail for many of the species.

Descriptions of the seeds of Southern African *Eugenia* species were mostly limited to vague comments pertaining to size, form and colour. In their revisions for Southern Africa, both Dümmer (1912) and White (1978) attached no obvious interspecific taxonomic significance to the seeds of this genus.

Material and Methods

Dried fruit from herbarium sheets was rehydrated by transferring to water and boiled for about 30 minutes. In rehydrated material, however, seed characteristics are not very reliable. If available, preference was thus given to fruits which were either fresh or preserved in formalin-acetic acid-alcohol (FAA).

All material was identified according to the criteria used in the original descriptions of the taxa and in most cases also by comparison with type specimens. The results are based on seeds from the following species:

GROUP X	GROUP Y
Eugenia capensis (Eckl. + Zeyh.) Sond.	*E. albanensis* Sond.
E. cf. *mossambicensis* Engl.	*E. erythrophylla* Strey
E. natalitia Sond.	*E. verdoorniae* Van Wyk
E. simii Dümmer	*E. woodii* Dümmer
	E. zeyheri Harv.
	E. zuluensis Dümmer

Results

Seeds of all the species possess a testa which is free from the pericarp and lies close to the surface of the embryo. The mature embryo consists of two apparently homogeneous, but in fact only partially fused, thick and fleshy plano-convex cotyledons, connected by a short radicular protuberance. A line of separation is visible on the more or less smooth surface of the embryo, between the cotyledons which lie side by side.

Apart from these mutual characteristics, species belonging to Group X differ in their seed structure from species belonging to Group Y. All the references to shape in the descriptions which follow, are based on seeds from fruits in which only one ovule had developed. If more than one ovule develops in the same fruit, the seeds are often variously compressed—this, however, is the exception rather than the rule.

GROUP X (Fig. 1): *Seed* (and embryo) reniform to subreniform, rarely oblong globose. *Testa* thin (c. 0,25 mm thick) and membranous, outer surface smooth,

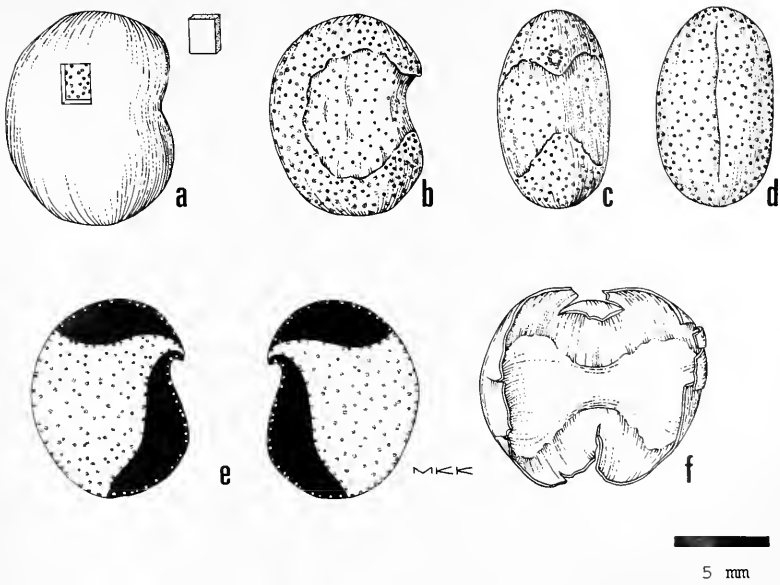

FIG. 1.
Seed morphology of *Eugenia natalitia* Sond.—GROUP X: a, seed with part of thin testa removed, showing surface of embryo beneath; b, lateral view of conspicuously glandular punctate embryo; c, ventral view of embryo showing spot of densely arranged glands on radicular protuberance; d, dorsal view of embryo showing the short line of separation between the two cotyledons; e, split-open embryo, showing region of fusion (black) between cotyledons; f, split-open testa, showing the slightly raised pattern on inner surface.

light brown; inner surface with a slightly raised, lighter-coloured pattern resembling in outline two horseshoes connected between the open ends. *Cotyledons* equal, bright green (when fresh), all the free surfaces conspicuously glandular-punctate, opposing faces more or less plane; the line of demarcation more or less straight; outer surface of each cotyledon with a horseshoe-shaped pattern due to a slightly depressed or irregular cotyledon surface with often slightly smaller and lesser glands than the remaining surface: this pattern corresponds with the one on the testa. *Radicular protuberance* with a circular dark-coloured spot from which the radicle probably grows on germination.

GROUP Y (Fig. 2): *Seed* (and embryo) globose to subglobose. *Testa* thick (c. 1,0 mm) and woody, outer surface of one hemisphere more or less smooth and light brown, the other half thinner, covered by remains of the pericarp, dark coloured; inner surface with a prominent depression, lined with a whitish tissue. *Cotyledons* equal to nearly equal, pale green to greenish-white (when fresh),

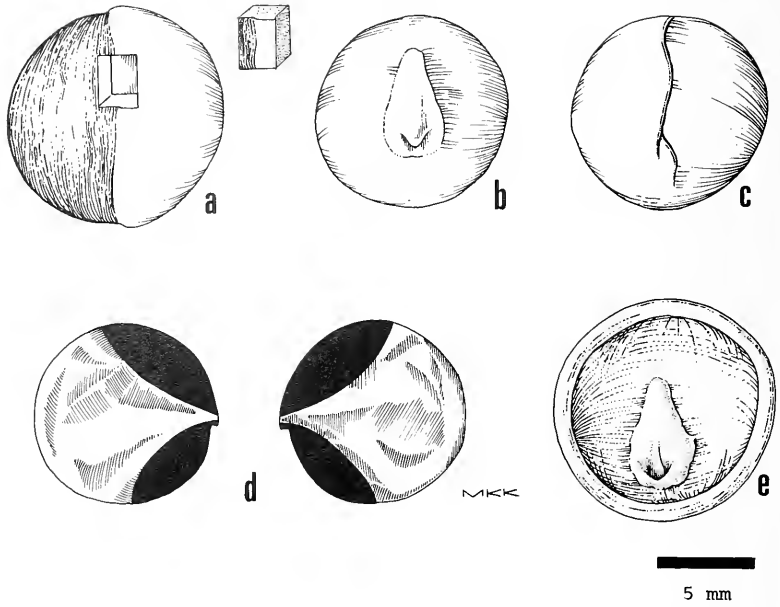

FIG. 2.
Seed morphology of *Eugenia zeyheri* Harv.—GROUP Y: a, seed with part of thick testa removed, showing embryo beneath; b, embryo with short radicular protuberance surrounded by a slightly raised light-coloured pattern; c, embryo with branched line of separation between the two cotyledons; d, split-open embryo, showing irregular inner surface of cotyledons and region of fusion (black); e, one half of testa, showing the light-coloured depressed pattern on inner surface.

apparently eglandular but usually with a few obscure glands mainly associated with the radicular protuberance; opposing faces usually somewhat concave or with ridges fitting into corresponding grooves, sometimes more or less plane; the line of demarcation straight, curved, or ramnified; outer surface of each cotyledon with a slightly raised, more or less linear, ovate or obovate, smooth-surfaced strip of tissue running around the radicular protuberance dorsally towards the start of the demarcation groove, fitting into the depression on the inner surface of the testa. *Radicular protuberance* with the spot from which the radicle grows (cf. Group X) probably present, but obscure.

DISCUSSION

The division of the Southern African *Eugenia* species into two groups on the basis of anatomical characteristics is correlated with two morphologically different

kinds of seed. This points towards the existence of at least two major lines of evolution in the local members of this genus.

It would appear that the species of Group X and Group Y are in fact not as closely related as was believed by previous authors. According to the present results the delimitation of some of the taxa proposed by White (1977, 1978) needs serious reconsideration.

Amshoff (1958) believed that the African members of *Eugenia* have the testa probably adhering to the pericarp, thus differing from the American members, in which the testa is free. This, however, was not confirmed by the present study. In all the species examined the testa remains on the cotyledons when the pericarp is removed. Furthermore, the seeds of Group X closely resemble those of *E. uniflora* L. from South America, which is the lectotype species for the genus *Eugenia* L.

For the present, no suggestions are made as to a formal taxonomic rank for Group X and Group Y. Features of much more African species need to be studied to ascertain the full taxonomic implications of these findings.

ACKNOWLEDGEMENTS

The author wishes to thank the Director and staff of the Botanical Research Institute in Pretoria for assistance provided in various ways, as well as Mrs M. Kingon who prepared the line drawings. The financial aid received from the South African C.S.I.R. is acknowledged with thanks.

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COLOUR DISCRIMINATION IN THE POLLINATION OF *PORTULACA GRANDIFLORA* HOOK., BY *APIS MELLIFERA* L.

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Abstract

Few data are available on colour discrimination by honeybees during actual pollination. The present work indicates that in *Portulaca grandiflora* the purple flowers are discriminated against, relative to yellow and orange flowers.

Uittreksel

KLEURONDERSKEID BY DIE BESTUIWING VAN *PORTULACA GRANDIFLORA* HOOK. DEUR *APIS MELLIFERA* L.

Min gegewens is beskikbaar oor die kleurvoorkeur van heuningbye gedurende bestuiwing. Die huidige werk dui daarop dat by *Portulaca grandiflora* daar teen die pers blomme gediskrimineer word ten gunste van geel en oranje blomme.

Introduction

In an insect-pollinated species, variation in flower colour is a particularly significant form of variation. This is because the evident adaptive significance of flower colour in relation to insect pollination suggests certain of the factors which may underlie the maintenance of the variation. This contrasts with most other forms of variation, such as the vast reserves of isoenzymic polymorphism revealed by electrophoretic studies, in which the factors maintaining the variation remain almost completely unknown.

The various ways in which flower colour variation may be maintained by pollination have been reviewed in detail by Mogford (1978). In outline, it is necessary first to distinguish between instances of polymorphisms and other forms of stable variation, and instances of variants maintained merely by recurrent mutation and removed by selection (Ford, 1975). Of the former categories, the principal consideration is whether certain of the types are subject to preferential pollination, in which case three types of situation may be distinguished:

(a) those situations maintained by some advantage which accrues from the favoured type being visited first;
(b) those situations where the overall level of pollination of the population is increased by the favoured types attracting higher numbers of pollinators, or encouraging foraging for longer periods; and
(c) those situations where the differences in attractiveness vary between pollinating species, thereby providing a degree of divergence in pollinator between the

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colour types. This is perhaps the most significant situation, in that the flower colour variation is acting as a means of cleaving the population into segregates between which there occurs limited gene flow. Accordingly, the variation is acting as a medium for sympatric evolutionary divergence with respect to the whole gene pool.

Records of colour discrimination during pollination are therefore of interest. Instances have been recorded in *Lantana camara* (Dronamraju, 1960), *Leavenworthia crassa* (Lloyd, 1969), *Raphanus raphanistrum* (Kay, 1976), *Cirsium palustre* and *Anagallis arvensis* (Mogford, 1972, 1974 a, b, 1978). However, few data are available on the discriminatory responses of the honeybee, *Apis mellifera* L., during pollination. The present work was therefore designed to study the possible occurrence of colour discrimination in the pollination of the rose moss, *Portulaca grandiflora* Hook., by honeybees.

Material and Methods

Observations were conducted during February and March, 1978, on a large bed of evenly spaced, single-flowered plants of *P. grandiflora* in Grahamstown Botanic Garden. The population consisted of a majority of purple-flowered plants, together with smaller numbers of red, yellow, and orange plants. No differences were observed between the colours except in pigmentation.

The population was visited almost exclusively by pollen- collecting honeybees. Foraging commenced when the bed was illuminated by direct sunlight, at about 09h00, at which time the flowers opened. The flowers remained open for only about three hours, despite continued illumination by direct sunlight. Competition for pollen was most intense among newly-opened flowers.

Observations were conducted over 14 mornings. In each case observations were restricted to within a marked area of 5 square metres. The number of flowers of each type within the area was counted prior to each period of observation, following which the visits of bees to flowers within the area were observed and classified with respect to colour. Individual bees were followed for as long as possible in order to reduce human bias in the choice of plants. A different marked area was used for each period of observation, in order to reduce the effects of any local differences in plant size.

For each period of observation, the number of flowers of each colour present within the plot, and the number of each colour visited by the honeybees, were recorded. Two analyses were used to determine the type of discrimination afforded to each colour:

(a) Comparisons were performed, using χ^2, of the observed and expected number of flowers of a particular colour visited. These tests were performed separately for each colour versus the other colours combined, in each period of observation.

(b) Considering the observations as a whole, χ^2 tests were used to compare the total number of times each colour was preferentially visited, to the total number of times the colour was discriminated against. These comparisons were based solely on the types of discrimination indicated by the percentage values for occurrence and visits, regardless of the individual significance of these values when considered per period of observation. The method therefore provided a cumulative measure of discrimination with respect to each colour.

Results

The results of analysis (a) are shown in Table 1, and those of analysis (b) in Table 2.

Table 1.
Flower colour and bee visit ratios for *P. grandiflora*.

Plot	Flower Colour Ratio					Visits Ratio					Discrimination Probability			
	P	R	Y	O	n	P	R	Y	O	n	P	R	Y	O
1	70,2	0,0	11,9	17,9	84	65,2	0,0	13,6	12,2	66	NS	—	NS	NS
2	75,8	3,0	12,1	9,1	66	71,3	2,8	12,0	13,9	216	NS	NS	NS	NS
3	63,0	9,8	2,2	25,0	92	55,6	12,6	5,9	25,9	135	NS	NS	*	NS
4	68,1	9,0	16,1	6,8	279	56,4	8,3	16,5	18,8	133	(**)	NS	NS	***
5	51,7	14,8	5,4	28,1	203	42,0	17,8	4,0	36,2	174	(*)	NS	NS	*
6	53,6	36,0	10,4	0,0	125	52,8	31,8	15,3	0,0	176	NS	NS	NS	–
7	54,0	36,5	3,8	5,7	211	43,4	38,0	8,5	10,1	129	(*)	NS	**	*
8	50,4	45,7	3,9	0,0	129	43,7	49,2	7,0	0,0	199	NS	NS	NS	–
9	49,0	34,8	14,8	1,3	155	37,8	35,7	21,0	5,6	143	(**)	NS	NS	***
10	64,0	15,4	2,2	18,4	136	58,7	17,5	7,3	16,5	206	NS	NS	***	NS
11	60,9	15,4	0,6	23,1	156	37,6	15,4	1,7	45,3	117	(***)	NS	NS	***
12	52,3	34,6	2,0	11,1	153	55,6	26,6	6,5	11,3	124	NS	NS	**	NS
13	75,8	3,0	12,1	9,1	66	70,7	3,0	12,0	14,3	133	NS	NS	NS	NS
14	70,8	8,8	4,4	16,2	68	44,8	11,9	11,9	31,3	67	(***)	NS	**	**

Ratios listed as percentage values based on sample size n.
Probability values calculated as described in text, analysis (a).
Unbracketed probability values indicate colours discriminated against.

* = significant at 5 % level
** = significant at 1 % level
*** = significant at 0,1 % level.

Colour Type	*Favoured*	*Neglected*	*Probability*
Purple	1	13	(***)
Red	7	5	NS
Yellow	11	3	*
Orange	11	1	***

Table 2.
Cumulative analysis of pollination data for *P. grandiflora*. Values calculated as described in text, analysis (b). Probability values abbreviated as in Table 1.

Analysis (a) indicated discriminative visiting against the purple flowers, random visiting of the red flowers, and preferential visiting of the yellow and orange flowers. Thus, in six cases the purples were discriminated against, but in no case were they favoured; in contrast, the yellows were favoured five times, and never discriminated against, while the oranges were favoured six times, and never discriminated against.

The degrees of discrimination involved were small but quite consistent. Because of their individual smallness, analysis (b) was of particular value, and in fact confirmed the previous results, even to the extent of supporting the slight favouring of the orange over the yellow flowers suggested by the first analysis.

Discussion

Several workers have shown the ability of honeybees to discriminate between colours in artificial experiments (Goldsmith, 1961). However, the colour responses of bees during actual foraging have been little studied, principally because fewer circumstances are available in which discrimination between flowers can be ascribed specifically to colour rather than floral structure or patterning. The result has been to emphasise the difficulty, pointed out by Meeuse (1961), of knowing the degree to which bees actually use the powers of colour discrimination which they evidently possess. The use of flower colour variants, however, obviates the difficulty of differences in floral structure, and provides a useful index of bee behaviour in nature.

As such, the results are of value in showing the capacity of *A. mellifera* for discrimination of this type. This is of interest since work on the flower colour polymorphism of *Cirsium palustre* indicated that, in an instance where honeybees were studied, they failed to show colour discrimination, unlike the general results obtained for *C. palustre* with bumblebees (Mogford, 1974b).

There are in fact two components which might lead to the type of result obtained in the present work: colour discrimination *per se*, and apostatic effects in bee behaviour which would result in over-visiting of the most frequent colour. Such apostatic effects are a consequence of the fact that, if "search-image" responses for a specific colour are elicited by successive, random visits to two or more flowers of that colour, then such responses would be elicited for the more common variety to an extent greater than that represented merely by its relative frequency in the population. The most common colours would therefore be preferentially visited in a response quite apart from any such based on colour preference *per se*.

However, in the present work, the most frequent colour was in fact discriminated against, indicating that search image responses were likely to be of minimal importance. The same conclusion was reached in the study of the pollination of *Cirsium palustre* by bumblebees, by a method based on a comparison of bee visit sequences with heterogeneity in the distribution of colour types within populations

(Mogford, 1972). The present results may therefore be taken as indicating actual colour preference *per se*.

It is less certain whether pollination effects underlie the maintenance of the flower colour variation in *P. grandiflora*. The wide range of colours present in garden forms—which includes variation from pure white to yellow, rose, scarlet, deep red and purple (Bailey, 1930)—is undoubtedly maintained by the process of disruptive selection for flower colour variants practised by cultivators of all decorative species.

However, orange-flowered plants are known to be present in appreciable frequency among the typical purple-flowered plants in natural populations of the species in its native Brazil (Bailey, 1930). It is therefore quite probable that the presence of both orange and purple flowers constitutes a stable polymorphism in nature.

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RE-SURVEY OF THE ALIEN VEGETATION IN THE CAPE PENINSULA

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Abstract

A distribution study of woody alien species in 87 sample sites in the northern half of the Cape Peninsula was carried out in 1959/60 by Hall (1961). In 1976 the same sites were re-sampled to assess the change in distribution and infestation over the subsequent 16 years. The effects of clearing and fire were examined and it was concluded that there had been a small but definite increase in the infestations of some species. In spite of extensive clearing, *Pinus pinaster* remains the most widespread invasive alien species.

Uittreksel

HEROPNAME VAN DIE UITHEEMSE PLANTEGROEI IN DIE KAAPSE SKIEREILAND

'n Verspreidingsstudie van die houtagtige inheemse soorte in 87 monster persele in die noordelike helfte van die Kaapse Skiereiland is in 1959/60 deur Hall (1961) gedoen. Gedurende 1976 is heropnames in dieselfde persele gedoen om die verandering in vervuiling gedurende die voorafgaande 16 jaar te bepaal. Die invloed van opruiming en vuur is bestudeer en daar is tot die gevolgtrekking gekom dat daar in klein maar bepaalde toename in die vervuiling van sekere soorte was. Ten spyte van grootskaalse opruiming bly *Pinus pinaster* die mees wydverspreide uitheemse-, indringersoort.

Introduction

Between May 1959 and May 1960, Hall (1961) conducted an extensive survey of the distribution of woody alien species in the mountains of the northern part of the Cape Peninsula. He examined the distribution of species above the 500 ft (152 m) contour. In 1976 Hall's plots were re-assessed (by McLachlan) to establish what changes had occurred.

Sampling Methods

Hall (1961) selected an area of about 102 square kilometres for his survey. Intersections of the thousand yard grid lines of the 1951 Trigonometrical Survey Map were chosen as the sample sites. Only those points above the 500 foot (152 metre) contour, and not in plantations, were examined. The points were located in the field using an altimeter and prismatic compass. At each site altitude, soil type, moisture, aspect, post-burn age, numerically and physiognomically dominant indigenous species, and the average cover, height and density of the community was recorded. Alien plants were recorded in terms of their density within a radius of 200 yards (183 m) of the sample point. The survey was restricted to species

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whose arborescent life-form was likely to cause changes in the structure and species composition of the Cape flora.

The same sample points were re-located in 1976 using the Trigonometrical Survey Map and Hall's original site photographs. It was found that most of the sites could be located accurately using the photograph, and in most cases the beacon built by Hall, marking the exact location of the site, was also found. Data were collected in the same way as in 1959/60, though some additional information was also recorded; such as observations on clearing and the effects of fire.

Distribution Patterns

In 1959/60, the percentage occurrence of each alien species in the 87 samples was calculated and compared to the occurrence in 1976.

Table 1.
Percentage occurrence of alien species in the 87 sample sites.

	1959/60	1976
Pinus pinaster	82	75
Hakea gibbosa	21	27
Pinus pinea	6	4
Hakea sericea	9	12,5
Pinus radiata	11	5
Hakea suaveolens	11	9
Acacia cyclops	17	17
Acacia saligna	16	25
Eucalyptus sp.	4	5
Albizia lophantha	7	6
Acacia longifolia	7	8
Acacia melanoxylon	6	4
Pinus canariensis	0	5

It is apparent that *Pinus pinaster* is the most widely dispersed alien species in the study area, though it has not extended its range over the 16-year period. Two *Hakea* species (*H. gibbosa* and *H. sericea*) occur in a greater number of sites than was found in 1959/60. The *Acacia* species, especially *A. saligna*, have also apparently spread over the years, as has *Eucalyptus* and *Pinus canariensis*. For the other species the percentage occurrence has changed very little. *A. cyclops* has apparently not increased much over the last sixteen years. The data for *A. longifolia* show that this species has not spread, though it has apparently spread in areas outside the sample sites (Moll & Campbell, 1976).

The distribution patterns of the introduced species in 1959/60 and 1976 are summarized and compared in Figs 6–14. The aliens are grouped into density classes as follows: 1–19, 20–50, 51–200, 200 + trees within a 200 yard (183 m) radius of the sample point.

Pinus pinaster is the most widely dispersed of all the introduced species and occurred in 82% of the sites examined in 1959/60 and 75% of the sites in 1976. It is more-or-less evenly distributed over the 102 square km of the study area, with occasional dense stands in some areas (see Fig. 6). The pattern of distribution of *P. pinaster* has altered over the 16 years; in 15% of the sites the density has drastically increased, and in 32% of the sites the density has decreased. This decrease in density is due mainly to clearing. *P. canariensis* (Fig. 14) has appeared in a number of sites, but only isolated trees were found. *P. radiata* (Fig. 9) and *P. pinea* (Fig. 14), on the other hand, are found only in isolated areas and have not spread.

Hakea populations have definitely increased slightly over the 16 years, and isolated plants and dense clumps of the different species were found at previous *Hakea*-free sites (notably *H. gibbosa* and *H. sericea*). *Hakea* spp. occur mainly on the lower, drier, western slopes of Table Mountain and on the north-western slopes of Vlakkenberg, Skoorsteenkop and the Muizenberg Mountains (see Figs 7, 8 and 9).

Acacia cyclops is still extensively distributed on the lower western slopes of Skoorsteenkop, Noordhoek Peak and Spitzkop. This species has spread to a number of other sites especially where the soil has been disturbed. *A. saligna* has also spread rapidly to a number of previously uninfested sites at slightly higher altitudes on the Muizenberg Mountains and on Skoorsteenkop and Vlakkenberg (see Figs 10 and 11).

Albizia lophantha (Fig. 12) is found mainly at the sites surrounding the Houtbaairivier valley and Orange Kloof. Apart from being found in broad-leaved scrub (McKenzie, Moll & Campbell, 1977) it also occurs on forest margins and in open forest (Moll & Campbell, 1976). Its spread has been checked by clearing in some sites. *Eucalyptus* sp. (Fig. 12) was found in a number of new sites where it has been planted as a windbreak or as isolated escapes.

Rate of Infestation

Only a few sites in the study area have been relatively undisturbed by man over the last 16 years. Five high altitude, relatively undisturbed sites of similar environments, with different size populations of *P. pinaster*, were chosen to gain an assessment of rate of infestation. These sites which had not been burned since 1959/60 were also far from *P. pinaster* plantations (which would provide an additional seed source). The density of trees at the five sites in 1959/60 and 1976 were compared, and the data are represented graphically (Fig. 1). The curve indicates the rate of infestation of *Pinus pinaster* from a single tree to the maximum density attainable (the steeper the slope of the curve, the faster the rate of spread). Initially the increase is relatively slow, until the population is some one

tree per 6 000 sq. m., then the increase in density is extremely rapid until the number of trees is about one tree per 40 sq. m. Once the pines have formed dense stands the rate of infestation slows until maximum density is attained. The 45° line on the graph indicates where "no change" occurs, and those sites below the line demonstrate the effects of clearing pines thus reducing spread. It is estimated that the time needed for one tree of *Pinus pinaster* to form a dense population will take from 35 to 45 years. At many sites young *P. pinaster* were found scattered in fynbos areas adjacent to dense stands and plantations. Thus the continued presence of these *P. pinaster* plantations and infestations on the mountains ensures a continued source of seed. The widespread distribution of *P. pinaster* is undoubtedly a result of its dispersal efficiency, and its ability to adapt to various habitats within the mountain fynbos biome.

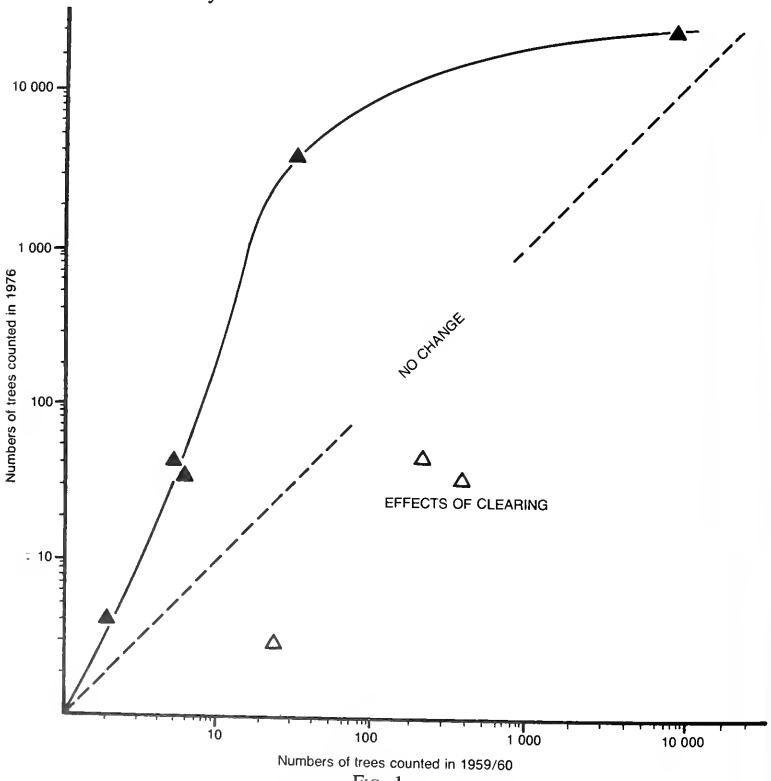

FIG. 1.
A graph comparing the numbers of trees counted in 1959/60 (▲) and 1976 (△) at five undisturbed sites. Three sites demonstrate the effects of clearing.

FIG. 2a. 1959/60

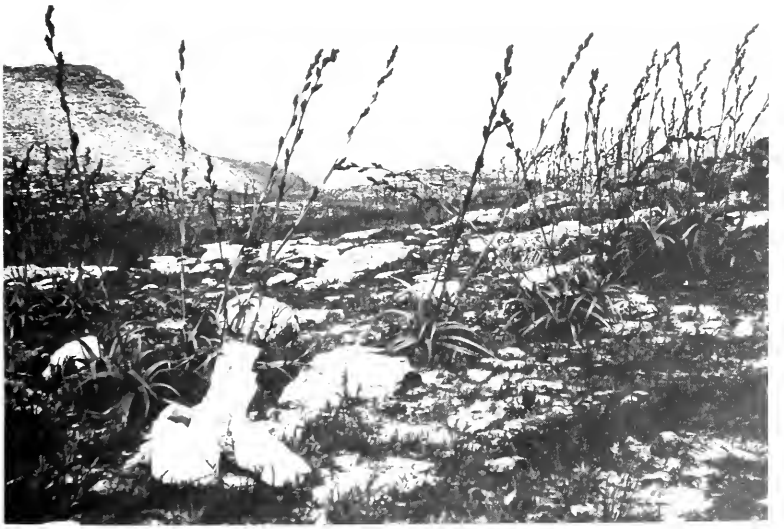

FIG. 2b. 1976

P. radiata is not considered to be an important pest, and although isolated trees were found in a number of sample sites in 1959/60 none were found in 1976 (see Fig. 9). The species does not spread rapidly and the isolated trees were probably cut down.

Hakea species on the other hand have a great potential for increase in population size because of the vast quantities of seeds produced. At many sites young, even-aged stands, that had been seeded from two or three adult plants which had died, occurred and dense stands were formed in some 1 to 5 years. Thereafter the density of the stand seems to remain static for a number of years if the area is left undisturbed. *Hakea sericea* and *H. gibbosa* characteristically form very dense stands (up to 150–250 plants per 100 m^2). Although the *Hakea* spp. occur mainly on the drier sandy and granitic soils, and were documented by Hall (1961) as being rare on moist slopes, their encroachment into new sites is occurring, and currently all species are also found in both relatively moist fynbos and in forest scrub. Many of the alien species, including *Hakea*, are rare at high altitudes. This is probably due to relatively slow dispersal rates and because the distance from seed sources is great, and is not due to habitat conditions precluding their growth.

It was noted that the *Acacia* species also occurred at a number of new sites at higher altitudes, especially *A. saligna* (Fig. 11), suggesting that these species also have the potential of spreading to a variety of mountain habitats. *A. longifolia* and *A. cyclops* showed their capacity to grow more densely in previously infested areas after clearing (see Figs 10 and 13). *A. longifolia* is also present in disturbed indigenous forest. Both species are common in areas where the soil has been disturbed. *A. melanoxylon* and *Albizia lophantha* are able to invade scrub and thrive in disturbed forest communities, though *A. melanoxylon* is probably only a real threat to riverine communities in the study area (see Figs 12 and 13).

At 15 sites there was a high percentage of seedlings of *Pinus pinaster, Acacia saligna* and all three *Hakea* species in areas nearly free of adult plants.

Another feature of most alien species found in the study area is the development of clumps or scattered stands of the same age. In *Hakea* this is particularly evident as mass seed dispersal and simultaneous germination is usually induced by fire or injury. In eight sites *Pinus pinaster* was noted to occur as clumps of similar aged individuals. This tends to indicate that dispersal of *P. pinaster* seed is not random, but that seeding rates or seedling regeneration is dependent upon specific environmental and/or physiological factors.

At each site where there was evidence of clearing of *Pinus pinaster* the approximate numbers of felled trees was noted. There was evidence of clearing at 46 of the sites visited. At 17 of these sites there was evidence of only a few isolated trees having being cut down, and at the remaining 28 sites there was evidence of extensive clearing. Of these 28 sites 14 showed that felling of *P. pinaster* had been effective in drastically reducing the population and the spread of

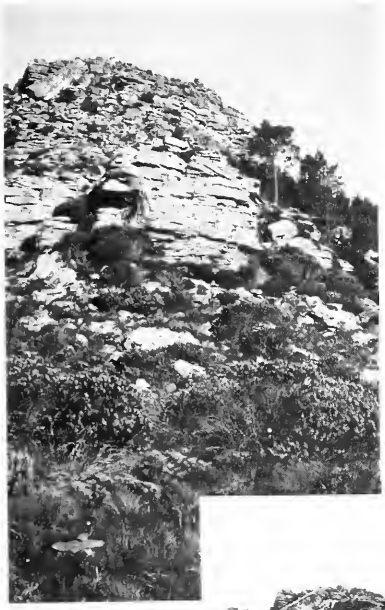

FIG. 3a. 1959/60

FIG. 3b. 1976

Comparative photographs showing areas cleared of *Pinus pinaster* at Bokkop.

this species. In areas where very dense stands had been felled and where 45 % of the cover is cut alien material, the regeneration of the indigenous flora is slow. In other areas where heavy cutting had taken place after 1959/60, but probably before about 1968, the regeneration of indigenous flora was apparently unaffected where the previous population of pines was less than one tree per 300 m^2. Two sites had been burnt after cutting and thus nearly all evidence of previous pine infestation in the area was destroyed. Here the fynbos appeared to be almost completely restored, with similar floristic composition at the previous infested areas as compared to previous near-free areas. This re-survey, therefore, seems to demonstrate that felling of *P. pinaster* is an effective measure of control.

Fire

Fire is of some significance in both the increase and decline of alien populations. It is generally known and well documented that the spread of *Hakea* spp., and to a lesser degree, *Acacia cyclops*, is aided by fire (see Stirton, 1978). With regard to *Pinus pinaster*, Adamson (1927) mentions that its invasive ability is greatly assisted by reduced competition from the fynbos brought about by frequent fires. In the sites examined this was not always the case. Some 32 % of the sites had been burnt in the last five years, of these there was evidence in nine sites of fire destroying *P. pinaster* trees. In four sites between 15 and 150 trees, 2–4 m high, were killed in the fires and this indicated that fire can be an important controlling factor in the spread of *P. pinaster* seedlings and young plants, as is also the case with *Hakea* seedlings. At one site half of the area had been recently burnt in a fire. The other half had not been burnt for at least 20–30 years and was infested with *P. pinaster* at about one tree per 250 m^2. In the burnt area, which had a high cover of *Mimetes*, not one pine seedling or tree was found.

Conclusions

In general, there has been a small but definite increase in the areas infested by *Hakea gibbosa, Hakea sericea, Acacia saligna, Pinus canariensis* and *Eucalyptus* sp. *P. pinaster* was found at somewhat fewer sites than before, and in most of the samples the density of *P. pinaster* had decreased. The felling of many dense stands of *P. pinaster* (see Figs. 2, 3 and 4) has without doubt drastically reduced the rate of spread in the study area, and probably more important is that large areas once lightly infested by *P. pinaster* have been cleared, thus preventing these areas from becoming densely infested.

A comparison of the density of *P. pinaster* and *H. gibbosa* over the 16-year period shows that in 1976 there were a few more sites having a low density of *P. pinaster* than in 1959/60, and that there is a general reduction in the densely infested areas. *H. gibbosa* data show that there are many more lightly infested sites, so the potential for spread is much higher (Fig. 5) *H. gibbosa* and

FIG. 4a. 1959/60

FIG. 4b. 1976

High rates of infestation by *Pinus pinaster* have occurred at some sites. In this case the beacon has been obscured by growth.

H. sericea have not, therefore, spread as much but are much more of a potential hazard as eradication of these species is much more difficult. It is of great concern that this survey indicates that there are large areas in the Cape Peninsula lightly infested—which have the potential of forming dense stands.

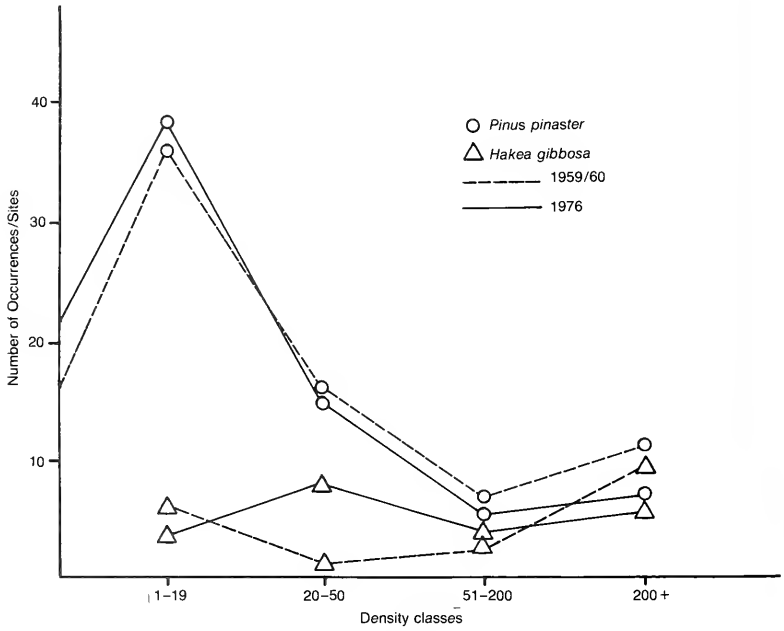

FIG. 5.
A graph comparing the number of sites at various class densities in 1959/60 and 1976. Class density is expressed as the number of plants within 183 m of the sample points.

Of all the alien species *P. pinaster* is by far the most efficient spreader in terms of area, but it can also be cleared relatively easily and effectively. Although large areas have been cleared, isolated trees and dense stands still remain in most areas and until these are cleared there will always be encroachment.

Alien species, which are more difficult to eradicate, even though some may spread more slowly, will also eventually encroach into most areas of the mountains in the future. Some of these species, such as *Hakea* spp., *Albiza lophantha* and *Acacia* spp., are able to form dense stands in many habitats. It is these species that will present a major problem, probably even more so than the present problem of the widely-distributed *P. pinaster*, in the future.

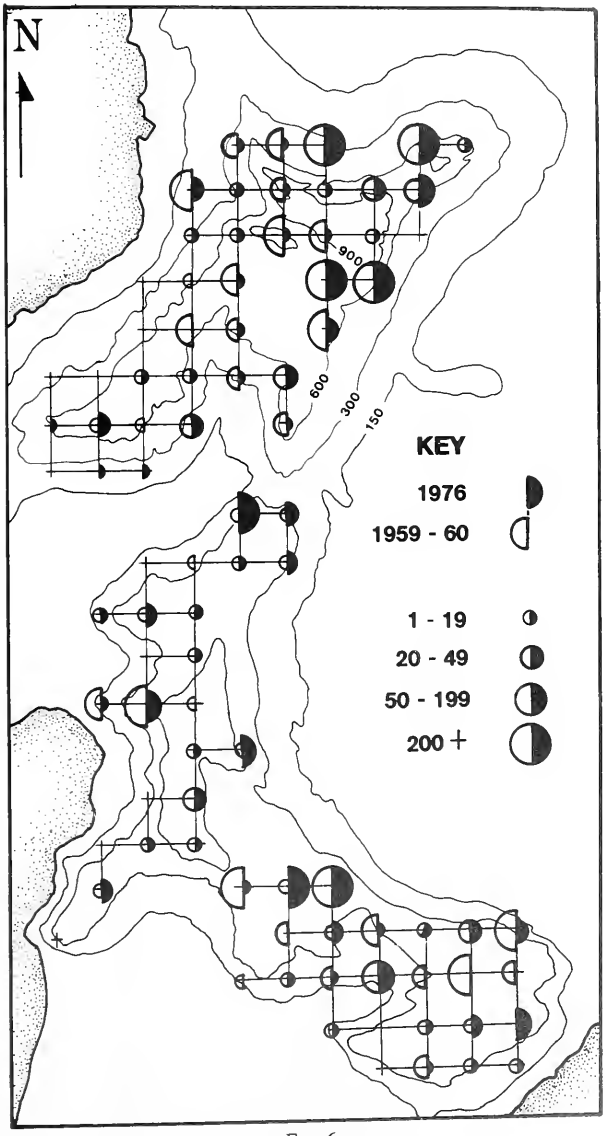

FIG. 6.
Pinus pinaster

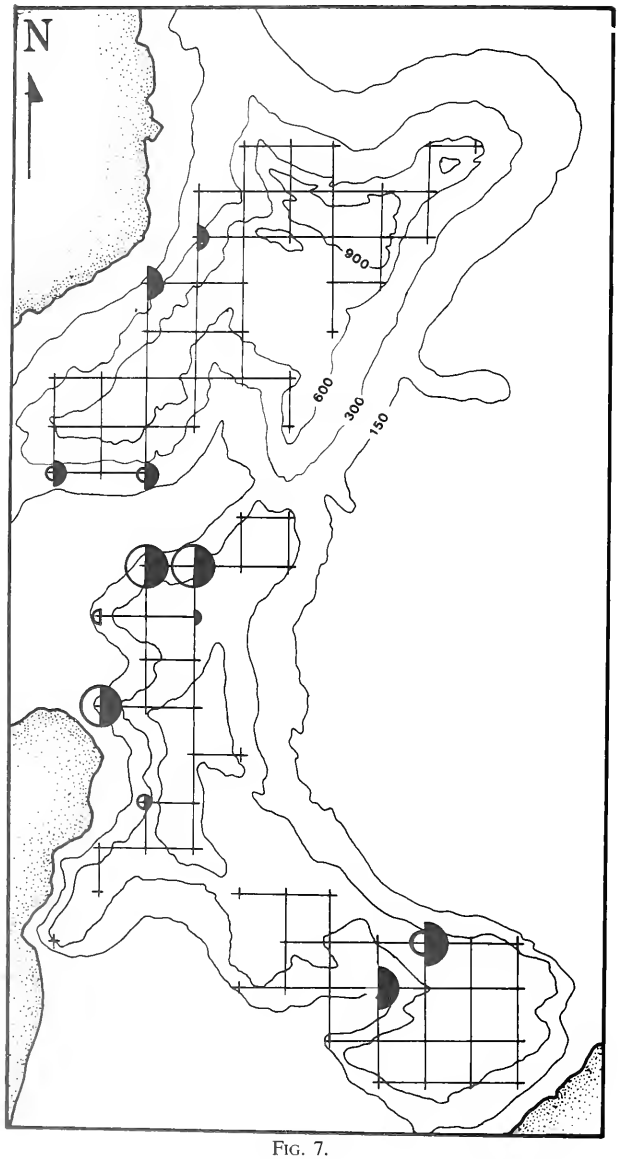

FIG. 7.
Hakea sericea

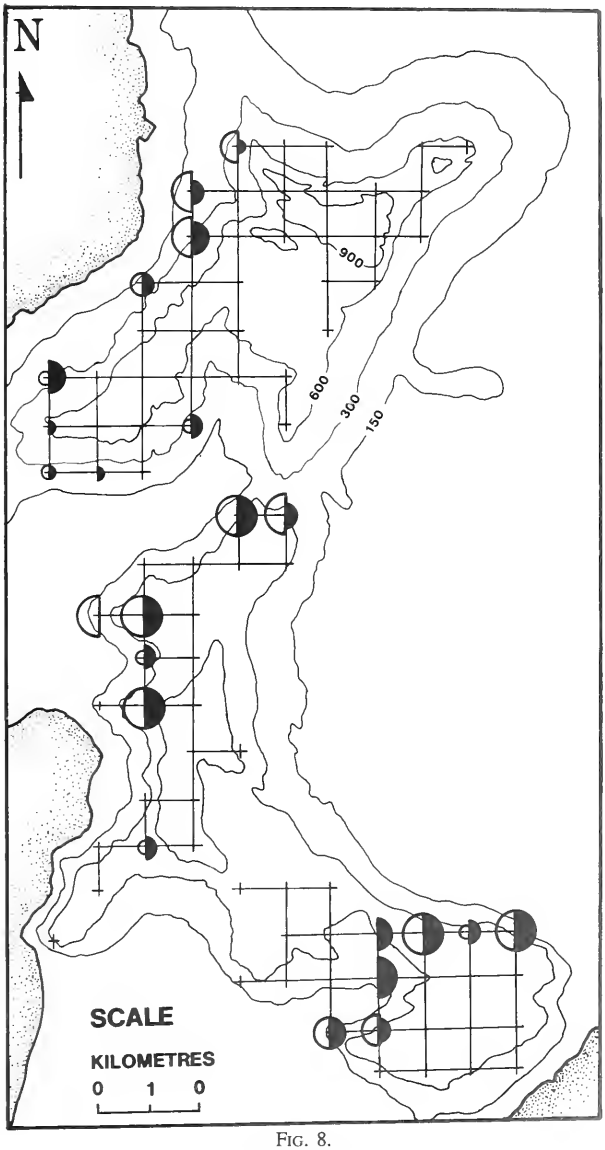

FIG. 8.
Hakea gibbosa

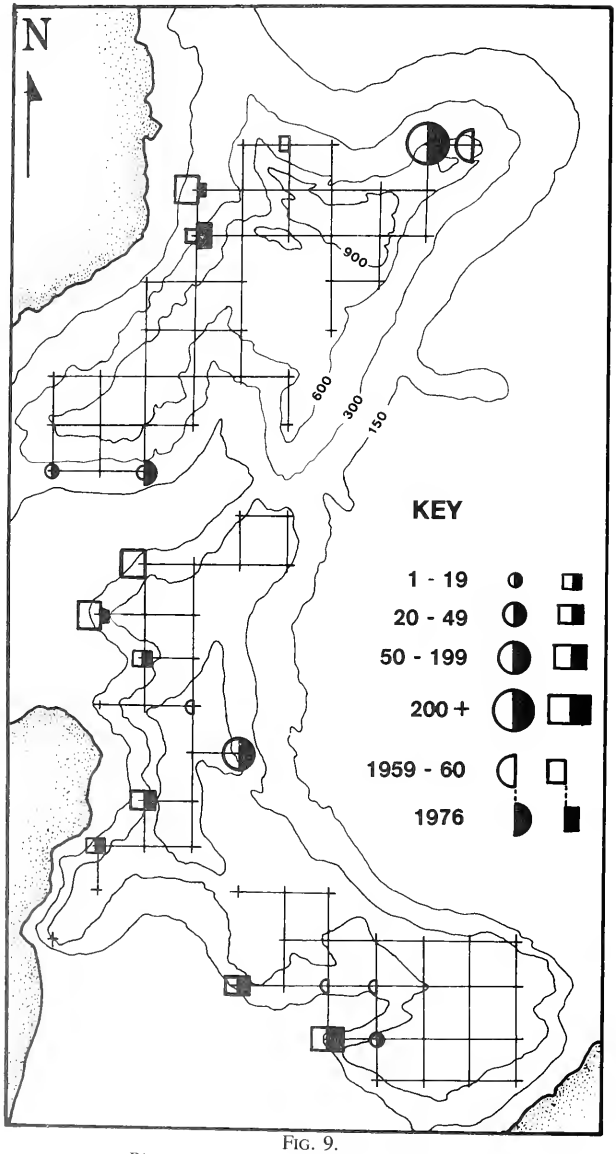

FIG. 9.
Pinus radiata ◑ *Hakea suaveolens* ◨

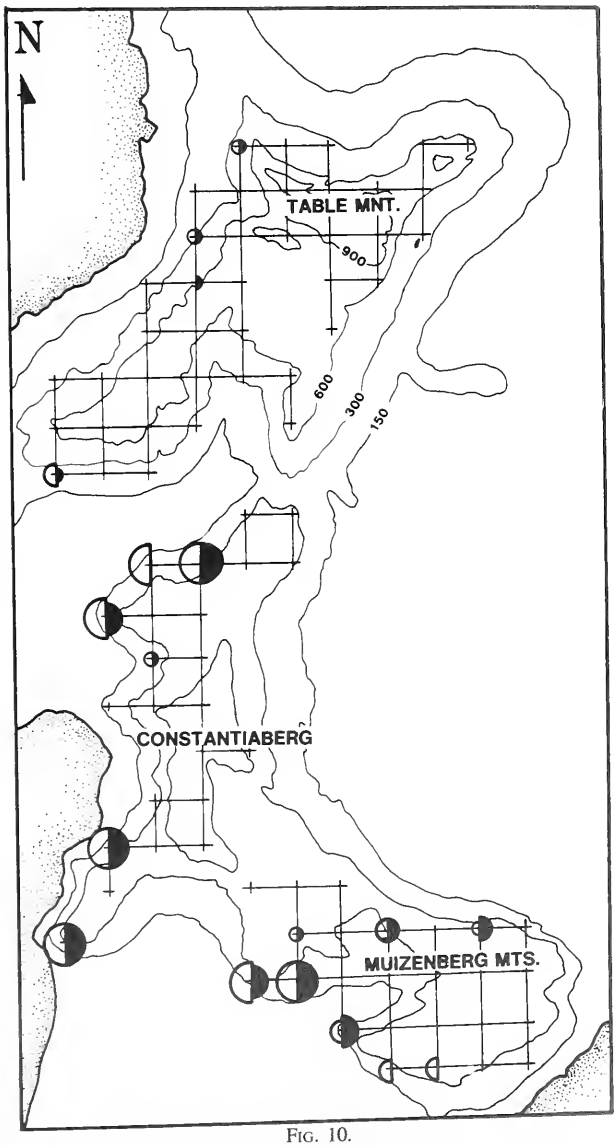

FIG. 10.
Acacia cyclops

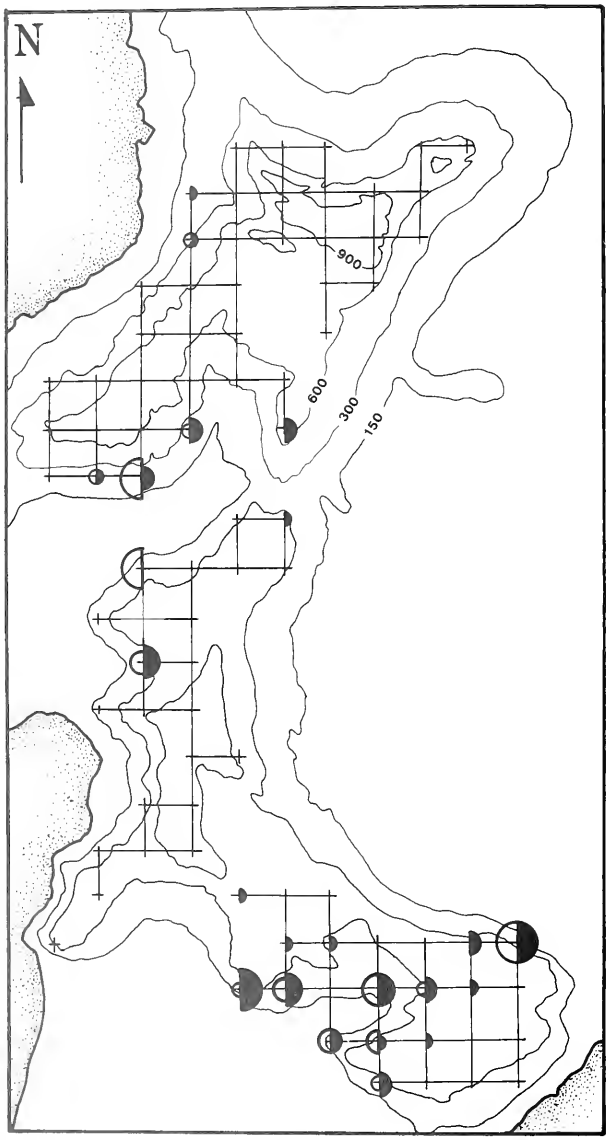

FIG. 11.
Acacia saligna

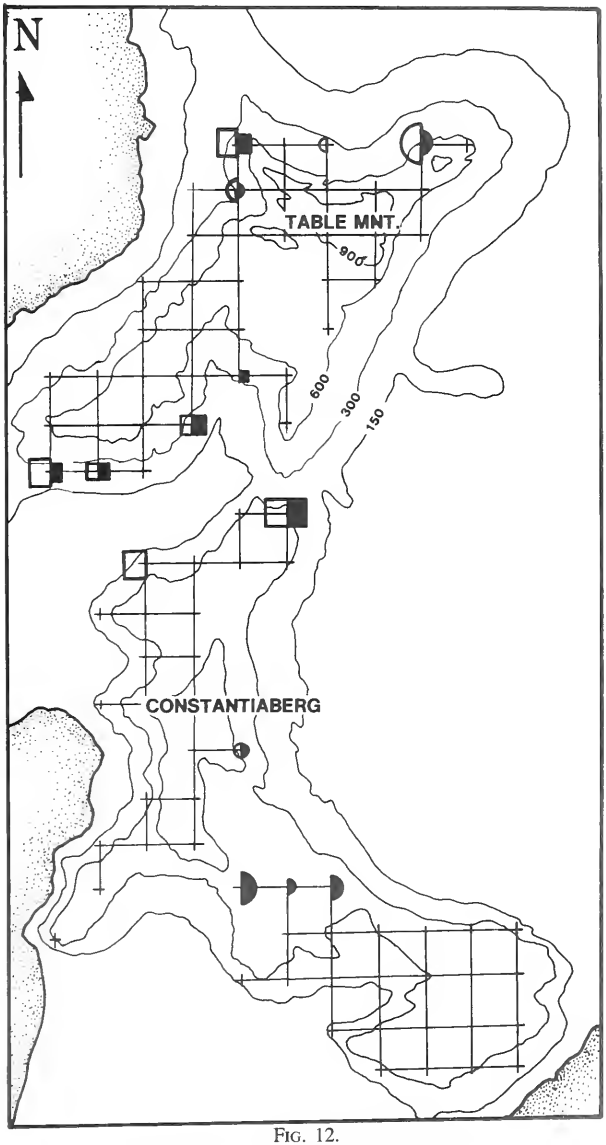

FIG. 12.
Eucalyptus sp. ◑ *Albizia lophantha* ◧

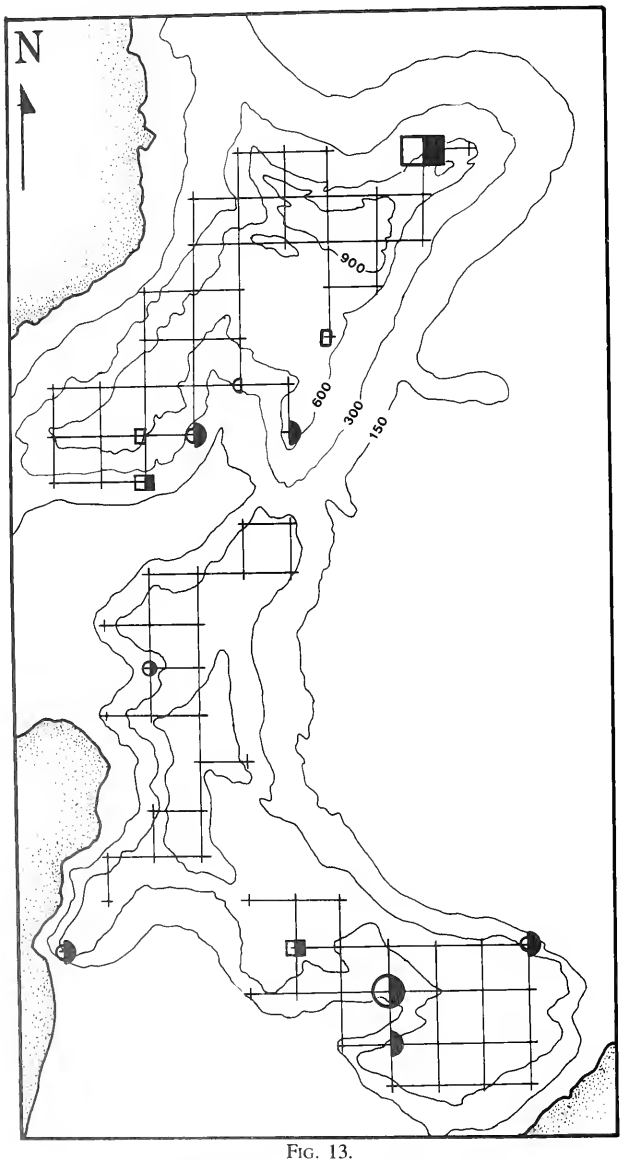

FIG. 13.
Acacia longifolia ◑ *Acacia melanoxylon*◧

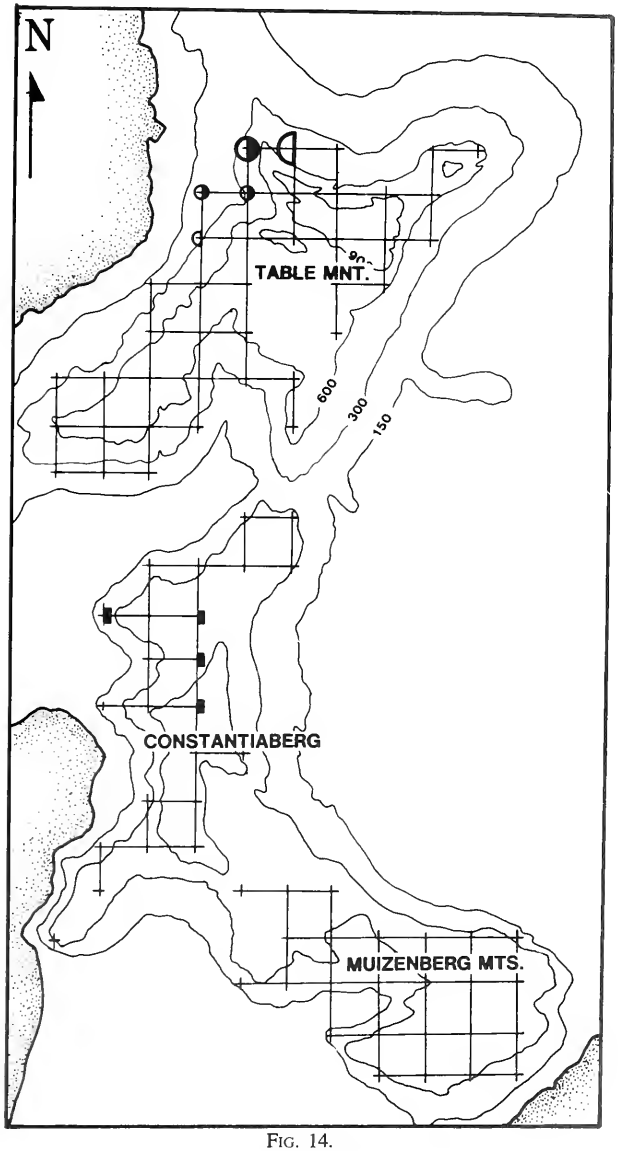

FIG. 14.
Pinus pinea ◑ *Pinus caneriensis* ◨

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FLAVONOID GLYCOSIDES OF *LEUCADENDRON* AND THEIR CHEMOTAXONOMIC SIGNIFICANCE

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Abstract

The flavonoid content of leaf material of 59 taxa of the genus *Leucadendron* (Proteaceae) was examined by two-dimensional paper chromatography. Most samples contained the 3-0-galactosides and 3-0-glucosides of quercetin and isorhamnetin while the rutinosides of these two aglycones were more restricted in their distribution, being found mainly in the *Leucadendron* section of this species. The 3-0-galactoside and 3-0-glucoside of myricetin were very restricted occurring only in a few species of the other section, *Alatosperma*. Cyanogenic compounds were detected for the first time in the Proteoideae (the South African sub-family of Proteaceae) and arbutin was also present in a limited number of species. The phenolic dilactone, leucodrin, was found in all taxa surveyed. The taxonomic significance of these distribution patterns as well as the phylogenetic implications are discussed.

Uittreksel

FLAVANOIEDE GLIKOSIEDES VAN *LEUCADENDRON* EN HULLE CHEMOTAKSONOMIESE BELANGRIKHEID

Die flavanoiede inhoud van die blaar van 59 taksons van die genus *Leucadendron* (Proteaceae) was ondersoek deur middel van twee-dimensionele papier chromatografie. Meeste van die monsters bevat die 3-0-galaktosiede en 3-0-glukosiede van kwersetien en isorhamnetien terwyl die rutinosiede van hierdie twee aglikone baie meer beperk was in hulle verspreiding aangesien hulle hoofsaaklik gevind word in die *Leucadendron* afdeling van spesies. Die 3-0-galaktosied en 3-0-glukosied van myrisetien was baie beperk en kom net voor in 'n paar spesies van die ander afdeling *Alatosperma*. Sianogeniese stowwe was vir die eerste keer gevind in die Proteoideae (die Suid-Afrikaanse onderafdeling van die Proteaceae) en arbutien was ook teenwoordig in beperkte getalle spesies. Die fenoliese dilaktoon, leucodrin, is ook gevind in al die taksons wat ondersoek was. Die taksonomiese belangrikheid en ook die filogenetiese gevolgtrekkings word bespreek.

Introduction

The genus *Leucadendron* was first defined as such in 1809 when Salisbury divided *Protea* into different genera. *Leucadendron* as well as *Protea* belong to the Proteoideae sub-family of the Proteaceae; it is in this sub-family where most of the South African members of the Proteaceae are found. Robert Brown in 1810 divided *Leucadendron* into several sections and with modification this division has held until the present time. The most recent taxonomic treatment of the genus *Leucadendron* was done by Ion J. M. Williams (1972) in which he recognized 91

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taxa. Williams divided the genus into two sections and 14 sub-sections. Included in his monograph is a worthwhile and interesting section on the taxonomic history of *Leucadendron*.

During a recent survey of some South African members of the Proteaceae for flavonoids and other phenolic compounds, several species of *Leucadendron* were examined. This paper reports the results of this examination and discusses the findings from a chemotaxonomic point of view. Several other workers have looked at the various phenolic compounds found in *Leucadendron* spp. at different times and this paper attempts to incorporate their results in the chemotaxonomic discussion.

Van Oudtshoorn (1963) found leucoanthocyanins in all 11 species of *Leucadendron* he examined, while Elsworth and Martin (1971) also found these compounds present in the 27 species of their study. The combined total of these two studies is 38 different *Leucadendron* spp. which produce anthocyanidins on acid hydrolysis. Quercetin and kaempferol were both found to have widespread distribution in these two studies while myricetin did not. Elsworth and Martin found myricetin present in only 5 of the 27 species examined, while Van Oudtshoorn reported 6 out of 11 species contained myricetin. Van Oudtshoorn also reported the presence of arbutin in all samples of unhydrolysed leaf material and hydroquinone present in the diethyl ether extracts of hydrolysed material.

There has been no report of cyanogenic compounds being found in *Leucadendron* spp.; in fact, the only report of HCN being produced by any plant in this sub-family was *Protea cynaroides* (Hegnauer, 1959). Another compound with restricted distribution is the phenolic dilactone leucodrin. Its structure was firmly established by Perold and Pachler (1966) and it has now been found in every species of *Leucadendron* examined and is characteristic of this genus (Plouvier, 1964; Murray and Bradshaw, 1966). Leucodrin has also been found in a few species of *Leucospermum* but the compound which is characteristic of this genus is conocarpin which is a diastereoisomer of leucodrin (Perold, Hodgkinson, Howard and Kruger, 1972).

The reasons that flavonoids are so widely used as taxonomic guides have been well documented by Harborne (1967, 1975). In the previous studies already mentioned, where flavonoid markers were used in chemotaxonomic studies involving this genus, only the aglycones were isolated and identified. In an attempt to broaden the scope of this type of study, the present work used unhydrolysed aqueous methanolic extracts of leaf material which allowed the flavonoid glycosides to be isolated and identified. This study is the first to give the genus *Leucadendron* an in-depth treatment from the chemotaxonomic point of view. Besides the flavonoid glycosides, the presence of arbutin and cyanogenic compounds, as well as leucodrin, are reported.

METHODS

The plant material was collected from the Botanical Research Institute, Pretoria and the National Botanic Gardens, Kirstenbosch. Voucher specimens are deposited in the herbaria of these two institutions. The material was either air-dried and milled before extraction with 80% methanol or the fresh material was ground in a Waring Blendor directly with 80% methanol. After extraction, the flavonoids were separated by paper chromatography and identified by the standard procedures of R_f values, acid hydrolysis and UV spectroscopy (Harborne, 1967). R_f values and UV spectral data for newly isolated flavonoids are found in Table 1; for information regarding other flavonoids reported in Table 2, but not described in Table 1 see Glennie (1979). All aglycone structures were confirmed by mass spectroscopy.

To determine the patterns of flavonoids present in the different plant samples, each sample was chromatographed two-dimensionally on Whatman No. 1 paper using PhOH (phenol : water–500:125) and 15% HOAc. The dried chromatograms were dipped in a solution of 3% $AlCl_3$ in methanol before air drying and viewing under a UV light. This converted the flavonoids from dull absorbing spots into bright yellow spots which were more easily and reliably scored.

All unhydrolysed plant extracts were examined for the presence of leucodrin, arbutin and hydroquinone by paper chromatography. Whatman No. 1 paper was pretreated with 10% glycerol in methanol and after a known amount of plant extract was spotted it was developed in BuOH : Tol (butanol : toluene–1:1 and

TABLE 1

R_f and spectral characteristics of some flavonoid glycosides of *Leucadendron*

Glycoside	R_f (x 100 on Whatman No. 1) in BAW	15% HOAc	H_2O	Phenol*
Quercetin-3-0-rutinoside	40	53	28	46
Myricetin-3-0-galactoside	12	20	11	19
Myricetin-3-0-glucoside	14	26	08	29

Glycoside	$\lambda max^{(nm)\ in}$ 80% MeOH Band II	Band I
Quercetin-3-0-glycoside	256(265)†	358
Myricetin-3-0-glycoside	264	356

Glycoside	$\Delta\lambda max^{(nm)\ in}$ NaOAc Band II	$AlCl_3$ Band I	NaOMe Band I	H_3BO_4 Band I
Quercetin-3-0-glycoside	18	62	42	22
Myricetin-3-0-glycoside	6	67	decomposes	20

*BAW-organic layer of butanol : acetic acid : water (4:1:5);
15% HOAc—15% acetic acid; Phenol—500 g phenol in 125 g water.
†inflection.

TABLE 2

Distribution of phenol glycosides in *Leucadendron* species

Species Section LEUCADENDRON	QGal	QGlu	QRut	IGal	IGlu	Compounds IRut	Compounds IAra	MGal	MGlu	CNg	Arb
Sub-section VILLOSA Williams											
L. coriaceum Phillips & Hutch.	+	+		+	+						
L. brunioides Meisn.	+	+		+	+						
L. stellare (Sims) Sweet	+			+						+	
L. levisanus (L) Berg.	+	+		+	+						
L. linifolium (Jacq.) R. Br.	+	+		+	+						
L. galpinii Phillips & Hutch.	+			+		+					
L. dubium Buek ex Phillips & Hutch.	+	+		+	+						
Sub-section MEMBRANACEA Williams											
L. remotum Williams	+	+		+	+						
L. pubescens R. Br.			+			+					
L. arcuatum (Lam.) Williams		+	+	+		+					
Sub-section NERVOSA Williams											
L. nervosum Phillips & Hutch.	+	+		+	+						
Sub-section LEUCADENDRON											
L. dregei E. Mey ex Meisn.			+								+
L. album (Thunb.) Fourcade	+	+		+	+						
L. rubrum Burm f. Prodr.	+	+		+	+						
L. argenteum (L.) R. Br.	+										
Sub-section CUNEATA Williams											
L. verticillatum (Thunb.) Meisn.	+			+	+						
L. corymbosum Berg.				+	+						
L. laxum Williams			+	+	+	+					
Sub-section NUCIFERA Williams											
L. sheilae Williams	+	+		+	+					+	
L. glaberrimum (Schltr.) Compton	+	+		+	+					+	
L. loranthifolium (Salisb. ex Knight) Williams	+	+		+	+					+	
L. roodii Phillips	+	+		+	+					+	
L. cadens Williams			+							+	
L. gydoense Williams			+			+				+	
L. sessile R. Br.			+							+	
L. daphnoides (Thunb.) Meisn.	+	+		+	+						+
L. barkerae Williams			+							+	
L. burchellii Williams			+							+	
L. tradouwense Williams			+			+				+	
L. tinctum Williams			+			+				+	

Sub-section VENTRICOSA Williams											
L. chamelaea (Lam.) Williams	+		+			+					
Section ALATOSPERMA Williams											
Sub-section TRIGONA Williams											
L. floridum R. Br.	+	+		+	+						
L. uliginosum R. Br.	+	+	+		+						
L. uliginosum ssp. *glabratum* Williams	+	+	+		+						
L. rourkei Williams	+	+		+	+						
L. conicum (Lam.) Williams	+	+		+	+						
L. salicifolium (Salisb.) Williams	+	+		+	+		+			+	
Sub-section BRUNNEOBRACTEATA Williams											
L. microcephalum (Gandoger) Gandoger & Schinz	+	+		+	+			+	+		+
Sub-section ALATA Williams											
L. xanthoconus (O. Ktze.) K. Schum.	+	+		+	+			+	+		
L. lanigerum Buek ex Meisn.											
L. var *laevigatum* Meisn.		+									+
L. modestum Williams		+				+					+
L. diemontianum Williams	+	+		+	+		+				+
L. flexosum Williams	+	+		+	+						+
L. salignum Berg.	+	+		+	+					+	+
L. foedum Williams	+	+		+	+						
L. procerum (Salisb. ex Knight) Williams	+	+		+	+						
L. discolor Phillips and Hutchinson	+	+		+	+						+
L. cryptocephalum Guthrie	+			+						+	+
L. eucalyptifolium Buek. ex Meisn.	+			+							+
L. gandogeri Schinz ex Gandoger	+	+		+	+			+	+	+	
L. strobilinum (L.) Druce	+	+		+							
L. spissifolium (Salisb. ex Knight) Williams	+	+	+	+	+	+				+	
L. spissifolium ssp. *fragrans* Williams	+	+		+	+	+				+	
L. spissifolium ssp. *phillipsii* (Hutchinson) Williams	+	+		+	+					+	
L. spissifolium ssp. *natalense* (Thode & Gilg.) Williams	+	+		+	+					+	
L. spissifolium ssp. *oribinum* Williams				+	+						
Sub-section COMPRESSA Williams											
L. teretifolium (Andrews) Williams	+	+		+	+	+				+	
L. nobile Williams	+	+		+	+					+	
L. muirii Phillips	+	+								+	
L. platyspermum R. Br.	+			+		+					+

Key: QGal Quercetin 3-galactoside; QGlu quercetin 3-glucoside;
QRut quercetin 3-rutinoside; IGal isorhamnetin 3-galactoside;
IGlu isorhamnetin 3-glucoside; IRut isorhamnetin 3-rutinoside;
IAra isorhamnetin 3-arabinoside; MGal myricetin 3-galactoside;
MGlu myricetin 3-glucoside; CNg cyanogenic compound;
Arb arbutin.

saturated with H_2O). After air-drying, the chromatograms were sprayed with Pauly's Reagent (0,5 % solution of diazotised sulphanilic acid in 10 % aqueous Na_2CO_3). The extracts were also examined for cyanogenic compounds using methods previously described (Glennie and Davidson, 1978). The presence or absence of hydroquinone is not reported in this paper as it is probably an artifact produced by the breakdown of arbutin.

Discussion

The distribution of the different phenolic glycosides throughout 12 of the 14 sub-sections is shown in Table 2. The table covers 59 of the 91 taxa suggested by Williams (1972) and the table is set out according to his arrangement of the genus. All the plants listed have been screened for all the compounds listed and only positive results presented. Blanks in the table represent negative results.

The most common flavonoid aglycones found in this study were quercetin and isorhamnetin and they were found singly or together in every sample examined. The glucosides and galactosides of these aglycones were the most prominent glycoside forms and occurred in over 50 % of the taxa listed in Table 2. Another reasonably common glycoside was the rutinoside of both quercetin and isorhamnetin. The other flavonoids listed occurred rarely.

The results from this chemotaxonomic study support the division of the genus *Leucadendron* into sections and sub-sections as suggested by Williams. The major flavonoids found in most sub-sections were the galactosides and glucosides of quercetin and isorhamnetin. The rutinosides of these two aglycones were found mainly in the *Leucadendron* section while the myricetin glycosides were found only in the *Alatosperma* section. This latter point is contrary to Williams' work as he suggested that this section contains the more advanced species while myricetin has traditionally been treated as a primitive character.

Sub-section *Nucifera* is characterized by containing mainly the rutinosides of quercetin and isorhamnetin with fewer species containing the flavonol galactosides and glucosides. Another chemical marker delimiting this sub-species is cyanogenesis which is widespread throughout. Cyanogenesis also characterizes the sub-sections *Alata* and *Compressa* where it is widespread. Species of *Alata* are also characterized by containing arbutin while most other sub-sections do not.

L. spissifolium is found in the *Alata* sub-section and this species is broken down into several sub-species most of which are reported in Table 2. The table shows that most of the sub-species contain only the galactosides and glucosides of the two flavonol aglycones while two sub-species contain the rutinosides as well. This chemical evidence supports Williams' grouping of the sub-species. The ssp. *oribinum* contains only isorhamnetin and also differs from the other sub-species in that it does not contain cyanogenic compounds.

Placed next to the *Alata* sub-section is the *Compressa* sub-section. This sub-section has the usual complement of flavonoids but like the species in *Alata*

some species contain HCN producing compounds and one species even contains arbutin.

It is of interest that this is the first genus of the sub-family Proteoideae (contains predominantly South African species of Proteaceae) which shows a positive reaction when tested for cyanogenic compounds. Proteas growing in the summer rainfall region (Glennie and Davidson, 1978) and all species of *Leucospermum* examined (Glennie, 1979) gave negative results when tested for cyanogenesis. The ability to produce HCN appears to predominate in the Grevilleoideae which is the sub-family which contains mostly Australian species. Hegnauer (1964) reported 16 different species from Grevilleoideae which gave positive results when tested for HCN production.

In the genus *Leucadendron* cyanogenic compounds are restricted to five of the ten sub-sections tested. In the sub-section *Nucifera* all species examined were positive for HCN except *L. daphnoides* which again was the only species examined from this sub-section to contain arbutin. Sub-sections *Alata* and *Compressa* are the only other sub-sections where cyanogenesis is common.

Arbutin occurs sporadically throughout many sub-sections of *Leucadendron* occurring mainly in the sub-section *Alata*; it occurs in 8 out of 14 species examined and tends not to be present in those species which are HCN producers. Van Oudtshoorn reported arbutin present in all 11 species of *Leucadendron* he examined but he also reported it present in *Leucospermum* while I could find none in this genus. *Protea* is the only genus examined by the present author which is rich in arbutin and other compounds related to this hydroquinone glucoside.

All taxa of *Leucadendron* examined in this study gave a positive test for leucodrin and many gave a positive reaction for leudrin (the dihydroxy form of leucodrin described by Highet, Perold and Sokoloski, 1976). The general occurrence of leucodrin throughout this genus could relate it to species found in the last 4 sections of *Leucospermum* as they also contain this unusual phenolic dilactone. Based on flavonoid evidence there is a great deal of similarity between the two genera. Both contain only flavonols which suggests that from a phylogenetic point of view they are relatively primitive plants. Also, another similarity is the 3-0-point of attachment of the sugars which is the only glycoside attachment pattern found in both genera.

Another property in common is that both genera contain chiefly quercetin and isorhamnetin as aglycones with a very few species of each containing myricetin. It has been suggested that the presence of vicinal trihydroxy groups such as that found in myricetin is a primitive character in plant phylogeny (Harborne, 1967). Since more species of *Leucospermum* (5 out of 29 examined) contained myricetin than *Leucadendron* (3 species out of 59 examined) it could be suggested that *Leucospermum* is on the whole the more primitive of the two genera. This agrees with the findings of Elsworth and Martin and the distribution pattern of leucodrin reinforces this idea. It also supports the possibility that *Leucadendron* as a genus

could have arisen from ancestors found in the more advanced sections of the genus *Leucospermum* (Rourke). However, this does not agree with the work of Johnson and Briggs (1975) who give *Leucadendron* and *Leucospermum* different ancestral types.

While comparing the flavonoid pattern of the two genera it should be pointed out that all *Leucospermum* spp. examined contained the rutinosides of quercetin and isorhamnetin while the rutinosides of these two aglycones occurred only sporadically in *Leucadendron*. Also, the arabinosides were common in *Leucospermum* but appear to be extremely rare in *Leucadendron*. The total flavonoid pattern of these two genera showed that they have many properties in common and are probably closely related but there are sufficient differences to separate them.

Leucoanthocyanins have been reported from all members of *Leucadendron* examined by Van Oudtshoorn and Elsworth and Martin. Because of this and also since it has been well documented that many members of the Proteaceae have been used as a source of tannin, the presence or absence of leucoanthocyanins has not been reported here. In view of the large amounts of anthocyanidins that are released on acid hydrolysis, it is probable that the tannins found in *Leucadendron* spp. are of the condensed type.

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A REVISION OF *THAMINOPHYLLUM* HARV. (ASTERACEAE—ANTHEMIDEAE)

Pauline Bond
(Compton Herbarium, Kirstenbosch)

Abstract

A revision of *Thaminophyllum* has been undertaken; three species are recognised. A key to the species is provided and a distribution map for each species is given.

Uittreksel

'N HERSIENING VAN *THAMINOPHYLLUM* HARV. (ASTERACEAE—ANTHEMIDEAE)

Die geslag *Thaminophyllum* is hersien en 3 soorte erken. 'n Sleutel tot die soorte en verspreidingskaarte vir elke soort word aangebied.

Introduction

Thaminophyllum, comprising three species, is a genus of small, branching, aromatic shrublets, endemic to the south-western Cape. The original description of the genus was given by W. H. Harvey in Harvey and Sonder's *Flora Capensis* **3:** 155 (1865). Two species were described. A third species has since been discovered and is described in this study.

Derivation of Name

Thaminophyllum is derived from the Greek θαμινος (crowded or close-set) and φυλλον (leaf).

Relationship with Other Genera

The genus was placed in the tribe Anthemideae by Harvey (l.c.). With this I concur. The aromatic scent, pluriseriate involucre, truncate style-branches and the absence of a pappus, agree with the characters of the tribe. If the artificial division of Anthemideae into 2 sub-tribes, Anthemidinae and Chrysanthemidinae (Hoffmann 1891:268) be accepted, *Thaminophyllum* would fall into the latter on account of the epaleate receptacle. There is a strong vegetative resemblance to *Eriocephalus*, but there are important differences in the floral parts, namely in the absence of paleae on the receptacle, the sterile ray-florets and fertile disc-florets. There is also a difference in the chromosome number (Goldblatt, 1980).

Floral morphology links *Thaminophyllum* most closely with *Lidbeckia* and chemotaxonomy bears out the relationship (Bohlmann and Zdero, 1974). But

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Lidbeckia differs in having petiolate and lobed leaves and capitula borne on long peduncles. Unfortunately no chromosome count has yet been made of *Lidbeckia*.

Inezia is another related genus and it has the same $n = 10$ chromosome number as *Thaminophyllum*. The yellow colour of the rays and the fact that they are fertile would seem to separate them, as well as the geographical separation. *Inezia* occurs approximately 1 600 km to the north of Cape Town.

There is a chemical alliance between *Peyrousea* and *Thaminophyllum* (Bohlmann & Zdero, 1974) and also a distinct vegetative resemblance. Unfortunately there is no chromosome count as yet. The main difference lies in the absence of ray-florets in *Peyrousea*.

From *Phymaspermum* (especially *P. leptophyllum* DC.) it differs in having sterile ray-florets, achenes without ribs, hairy leaves and disc-florets with 4-lobed limb. There is also a superficial resemblance to *Cymbopappus* (especially *C. adenosolen* (Harv.) B. Nord.). However, *Thaminophyllum* differs in having sterile ray-florets, no pappus, entire leaves and different cypselas.

A Revision of *Thaminophyllum*

Thaminophyllum Harvey in Flora Capensis **3:** 155 (1865); Benth & Hook., Genera Plantarum **ii:** 423 (1873); Phill. in Genera of S. African Pl. 824 (1951); Dyer in Genera of S. African Pl. **1:** 705 (1975).

Type species : *T. multiflorum* Harv.

Small, branching shrublets. *Leaves* aromatic, ericoid, alternate, sessile, with pilose or silky pubescence. *Peduncles* solitary or in leafy cymes towards the ends of branches. *Capitula* heterogamous. *Involucre* campanulate or ovoid. *Involucral bracts* 2–3 seriate, silky-pubescent or pilose, apically somewhat purple in colour. *Receptacle* epaleate, pubescent or pilose, convex or conical. *Ray-florets* 2–11, ligulate, white or pink, sterile, with cylindric tube and elliptic or obovate lamina 2–3 times as long as the tube; style undivided, not much exserted; pappus 0. *Disc-florets* 10–60, yellow, bisexual, corolla-tube somewhat compressed, resin-dotted, with acute or rounded lobes; anthers 4, obtuse at base, with apical, oblong sterile appendages; style sub-terete with linear, truncate branches, bristle-tipped; achenes (immature) oblong, sub-angled, glabrous, crowned with a hardened conical or globose stylopodium; pappus 0.

Chromosome numbers: $2n = 20$ (Goldblatt, 1980)

Distribution

All three species occur in fynbos in the winter rainfall area in relatively cool, moist mesic situations, on the Hottentots Holland and neighbouring mountains of the south western Cape.

T. mundii and *T. latifolium* have both been found near sea level with upper altitudes of 830 m for the former and 290 m for the latter. *T. multiflorum* has been collected at altitudes ranging from 250 m to 800 m.

In *Flora Capensis* and in Hutchinson's *A Botanist in Southern Africa* (1946–62) the additional localities of George and Petermeintjies (Pietermeintjies) are cited. Harvey cites *T. multiflorum* as having been collected in the district of George by Alexander Prior. However, the sheet in the Kew Herbarium bears a tag on which is printed, "Hott. Holl.". Dr Hutchinson's record from Pietermeintjies (vide *A Botanist in Southern Africa*) or "between Matjesfontein and Karroopoort" on his collecting label, is almost certainly an error. M. E. Kensit's specimen of *T. latifolium* in the Bolus Herbarium (without number) is said to come from Uitenhage. It is not possible to state categorically that this is incorrect as I have not undertaken an exhaustive search in the area. But until such time as it may again be collected in that locality, the record is suspect. R. Schlechter's specimen of *T. mundii* (T. 'pauciflorum') from the Caledon Zwartberg, dates from 1894 and the species has not been collected again on that mountain. There is every likelihood that a more extensive search will bring it to light.

KEY TO THE SPECIES

(a) Leaves > 1,5 mm wide, verrucose when dry; lobes of the disc-florets obtuse ..... 1. **T. latifolium**
Leaves < 1,5 mm wide, not verrucose when dry; lobes of the disc-florets acute ...(b)
(b) Ray-florets 7–11; involucre campanulate ± 10 mm wide ..... 2. **T. multiflorum**
Ray-florets 2–4; involucre ovoid-oblong ± 4 mm wide ..... 3. **T. mundii**

1. **Thaminophyllum latifolium** Bond, sp. nov.

Type: Fernkloof Nature Reserve, Hermanus, south-facing stony slope, 21/10/1974, *E. R. Orchard 270* (NBG, holo.; BOL, G, K, L, M, MO, PRE, S, STE, iso.).

Differt a *T. multiflorum* et *T. mundii* foliis latioribus viridis, lobi floribus disci obtusi.

Branched suffrutex to 750 mm. Lower stems leafless, upper leafy, silky-pilose. Stems terminate in a solitary capitulum but two buds remain dormant below and may develop later. *Leaves* alternate, sessile, spreading, lanceolate 0,7–10 mm long, 1,50–3 mm wide, somewhat convex with recurved margins, apex with acute, glabrous callus. Upper surface silky-pilose, becoming glabrescent, verrucose when dry, lower surface densely silky-pubescent. *Peduncle* 10–30 mm long, silvery-pilose. *Involucre* campanulate, 4–7 mm long, 6–10 mm wide; involucral bracts 3-seriate, silvery-pilose, inner with hairy, purplish apices. *Receptacle* narrowly conical, pilose. *Ray-florets* 6–11, sterile; tube 4–5 mm long, whitish; lamina 6–7 mm long, 3–4 mm wide, rotund, emarginate, resin-dotted and veined, white or pink above, pinky-purple below; style undivided, ovary filiform; pappus 0. *Disc-florets* c. 40–50, bisexual; corolla ampullaceous, yellow, resin-dotted,

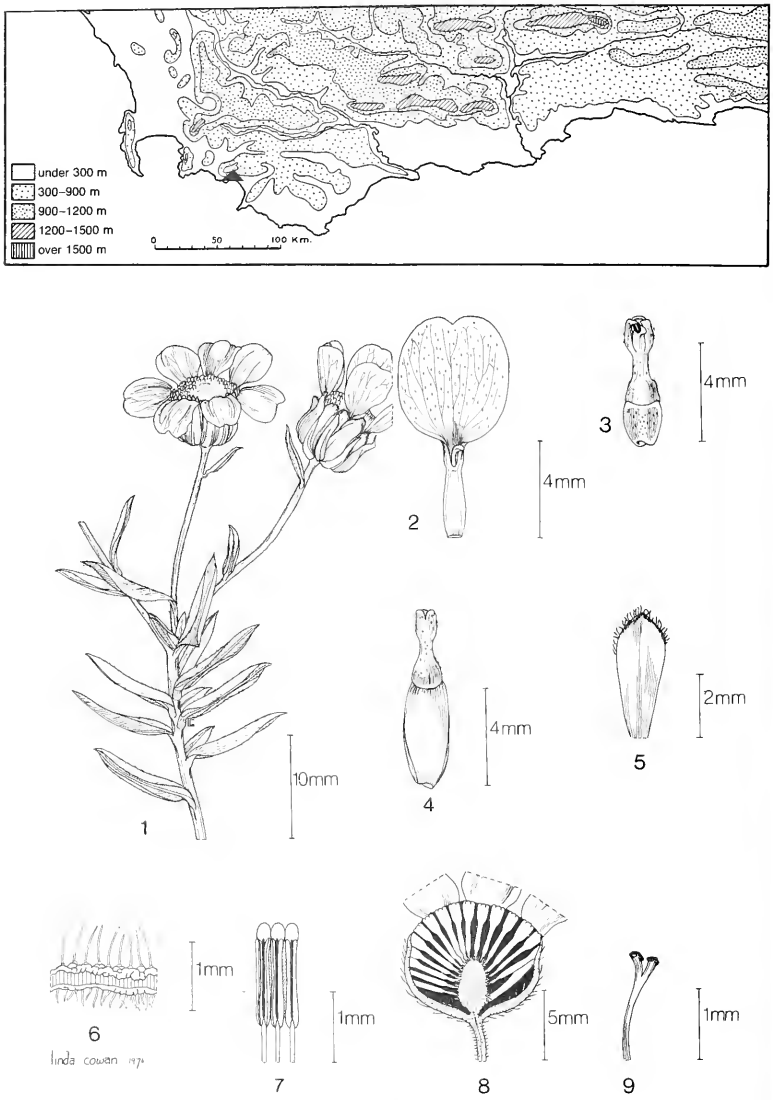

FIG. 1.
Thaminophyllum latifolium Bond. (1) Flowering shoot; (2) ray-floret; (3) disc-floret; (4) disc-floret, later stage; (5) inner bract; (6) cross-section of leaf; (7) anthers; (8) vertical section through capitulum (stylised); (9) upper portion of style and stigma. (From *Orchard 270*). Distribution map above.

3,25–4 mm long; lobes 4, oblong, obtuse, dark-edged; anthers 1,5 mm long or less, including the rounded apical appendage; style hardly exserted, terete with swollen base, style-branches darker, truncate, stigmatic surface bristly; cypselas elliptic, 2–2,50 mm long, 1–1,25 mm wide, light brown, furnished with a cream-coloured stylopodium; pappus 0.

Flowering period: August–December.

Distribution: *T. latifolium* is found on south-facing rocky slopes or along streamsides on the Klein River Mountains, Hermanus.

Diagnostic characters: The broad pink or white rays and broader, greener leaves make this an easily recognised species.

Specimens Examined

CAPE—3419 (Caledon): Fernkloof Nature Reserve, Hermanus (-AD), Oct., *Orchard 270* (NBG, holo.; BOL, G, K, L, M, MO, PRE, S, STE, iso.); above Voëlklip, Sept., *Esterhuysen 33604* (BOL, K, MO, PRE, STE); Hermanus, Nov., *Rogers 26534* (BOL, PRE); Vogelgat Nature Reserve, August, *Williams 2551* (K, MO, NBG, PRE); Hermanus, Nov., *Hayes Palmer* (NBG *28422*) (NBG); Hermanus, Sept., *Esterhuysen 33616* (BOL); the mountain above Hermanus, Nov., *Nordenstam & Lundgren 2254* (NBG, S); Voëlklip above 8th Avenue, Nov., *Bond 1697* (NBG).

2. **T. multiflorum** Harvey in Fl. Cap. **3:** 155 (1865).

Type: Cape: no precise locality, *G. Thom 834* (K!; NBG, photo.).

Branched suffrutex to 600 mm. Lower stems leafless, upper densely leafy and silky—pubescent. Stems terminate in a solitary capitulum but two buds remain dormant below and may develop later. *Leaves* alternate, sessile, ascending, somewhat incurved, linear-lanceolate, 0,9–1,2 mm long, 1 mm wide, margins becoming revolute, apex acute, midrib raised below. Both surfaces densely silky-pubescent. *Involucre* campanulate, 5–8 mm long, 9–11 mm wide; involucral bracts 3-seriate, silky-pubescent, outer shorter, inner with hairy, purple apices. *Receptacle* conical, pubescent. *Ray-florets* (7) 8–9 (10) sterile; tube 2–3 mm long, pale green, transparent, resin-dotted; lamina 5–7 mm long, 1,75–3 mm wide, obovate, emarginate or rounded, resin-dotted, white, faintly veined; style undivided; ovary elliptic; pappus 0. *Disc-florets* c. 50–60, bisexual; corolla tubular, yellow, resin-dotted, 1,5–2 mm long, lobes 4, acute, cucullate; anthers 1,25 mm long, including the rounded apical appendage; style terete with swollen base, style-branches truncate, stigmatic surface bristly; cypselas narrowly elliptic-oblong, somewhat four-edged, furnished with a yellowish stylopodium; pappus 0.

Flowering period: September–January.

Distribution: *T. multiflorum* appears to have a rather localised distribution, usually on south-west facing slopes of mountains in the Grabouw–Houw Hoek area.

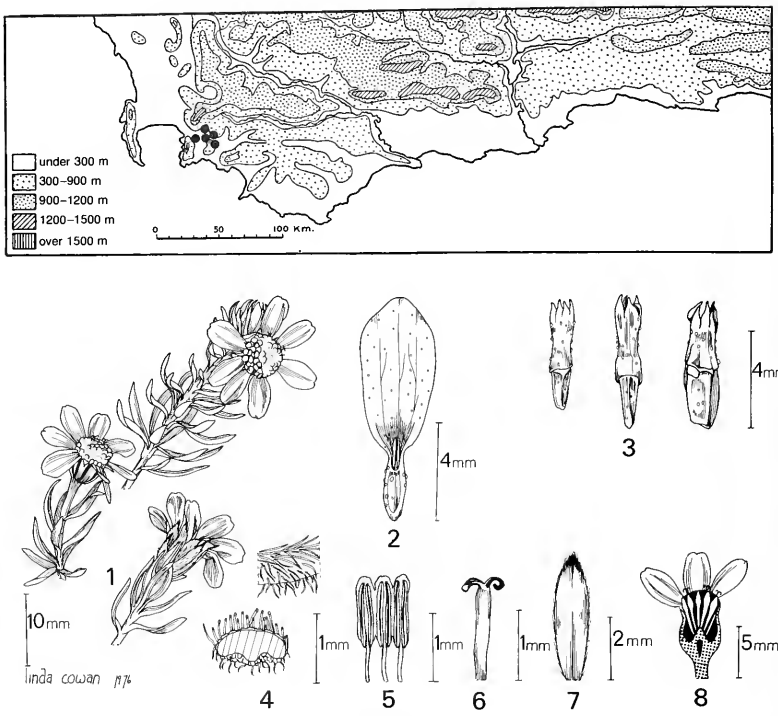

FIG. 2.
Thaminophyllum multiflorum Harv. (1) Flowering shoots; (2) ray-floret; (3) disc-florets at varying stages; (4) lower surface and cross-section of leaf; (5) anthers; (6) upper portion of style and stigma; (7) inner bract; (8) vertical section through capitulum (stylised). (From *Bond 1673*). Distribution map above.

Diagnostic characters: This species differs from *T. mundii* in the greater number of ray-florets (7–10), and the solitary capitula. It differs from *T. latifolium* in the narrower more silvery leaves and the narrower more constantly white ray-florets.

SPECIMENS EXAMINED

CAPE—3419 (Caledon): In clivis montis pone Houw Hoek (-AA), Oct., *H. Bolus 359* (BOL, PRE, SAM); Houw Hoek, Jan., *H. Bolus 4684* (SAM); in clivis montis pone Houw Hoek, Oct., *H. Bolus* Herb. Norm. *359* (BOL, PRE, SAM); Elgin, Sept., *L. Bolus s.n.* (BOL); Houw Hoek Forestry Reserve, Aug., *P. Bond 1673* (NBG, PRE); near Palmietriver north of Viljoenspas, Sept., *K. Bremer 121* (NBG, S); Aries Kraal, hill top, Nov., *R. H. Compton 16500* (NBG); Mt.

Lebanon, above De Rust, Oct., *E. Esterhuysen 33257* (BOL); Houw Hoek, Sept., *E. Esterhuysen 31109* (BOL); Houw Hoek Mountain, Sept., *E. Esterhuysen 32657* (BOL); Mountain Houw Hoek, Nov., *E. E. Galpin 4175* (PRE); Viljoen's Pass, Sept., *U. C. Gillett 4457* (BOL, GRA, PRE); Houw Hoek Mountain, Nov., *P. Goldblatt 3294* (MO, NBG); Houw Hoek, Sept., *P. Goldblatt 4982* (MO, NBG, PRE, S); Houw Hoek, July, *F. Guthrie s.n.* (NBG *28421*); Lebanon State Forest, Oct., *R. A. Haynes 717* (MO, NBG, PRE, STE); halfway up slope between Weir I and ridge, Lebanon, July, *F. J. Kruger KR 98* (PRE); Aries Kraal, Nov., *F. M. Leighton 765* (BOL, PRE); slopes of Groenland Mountains, above Lebanon Forest Reserve, Sept., *G. J. Lewis s.n.* (SAM *67567*); in montibus pr. Houw Hoek, Oct., *P. MacOwan 2953* (SAM); Houw Hoek Peak, Nov., *B. Nordenstam & J. Lundgren 2191* (NBG, S); Mts round Houw Hoek, Oct. *E. P. Phillips 56* (NBG); Viljoenspas, Sept., *S. Rehm s.n.* (STE *26530*); Houw Hoek's Berg, Oct., *R. Schlechter 5455* (BOL, GRA, PRE); Jakkalsrivier Experimental Catchment, Oct., *R. D. Smith 28* (STE); Viljoenspass, Sept., *R. G. Strey 743* (PRE); Palmiet River, Elgin, Dec., *T. P. Stokoe s.n.* (SAM *57027*); Grabouw, foothills of Palmiet River Mtns, Oct., *T. P. Stokoe s.n.* (SAM *62025*) (PRE, SAM, STE); Palmiet River, Elgin, Dec., *T. P. Stokoe 8151* (BOL); without locality, *G. Thom 834* (K).

Dubious localities: In provincia George, *Alexander Prior s.n.* (K, SAM). Although the SAM sheet bears a ticket in Pappe's handwriting recording the above locality, on the K sheet there is a tag on which is printed "Hott. Holl.", a far more likely locality.

As mentioned in the introduction, the locality "Between Matjesfontein and Karroo Poort" is almost certainly an error, for *J. Hutchinson 445* (BOL, GRA, PRE).

The epithet "multiflorum" refers to the number of disc-florets in each capitulum and not to the number of capitula in the inflorescence.

3. **T. mundii** Harvey in Fl. Cap. **3:** 155 (1865). *Type*: Cape: no precise locality, *Mund* (K!, NBG, photo.).

Much-branched suffrutex c. 450 mm high. Lower stems leafless, upper densely leafy, silky-pubescent with occasional long silky hairs. Stems terminate in a capitulum below which are c. 6–8 short leafy lateral branchlets, each ending in 1 or, rarely, 2 capitula. Leaves alternate, sessile, spreading, slightly twisted, linear-lanceolate, 7–8 mm long, 1 mm wide, margins revolute, apex acute, midrib raised below. Both surfaces densely silky-pubescent. *Involucre* ovoid-oblong, 4–5 mm long, 2–3 mm wide; involucral bracts 2–3 seriate, silky-pubescent, outer shorter, inner with hairy purplish apices. *Receptacle* slightly convex, pubescent. *Ray-florets* (2)3(4), sterile; tube 2–3 mm long, pale green, resin-dotted; lamina 5–7 mm long, 2–3 mm wide, elliptic, retuse or rounded, resin-dotted, white, veined; style undivided; ovary filiform; pappus 0. *Disc-florets* (11) 13–14 (-19), bisexual; corolla tubular, yellow, resin-dotted, 4–5 mm long; lobes 4, acute, cucullate;

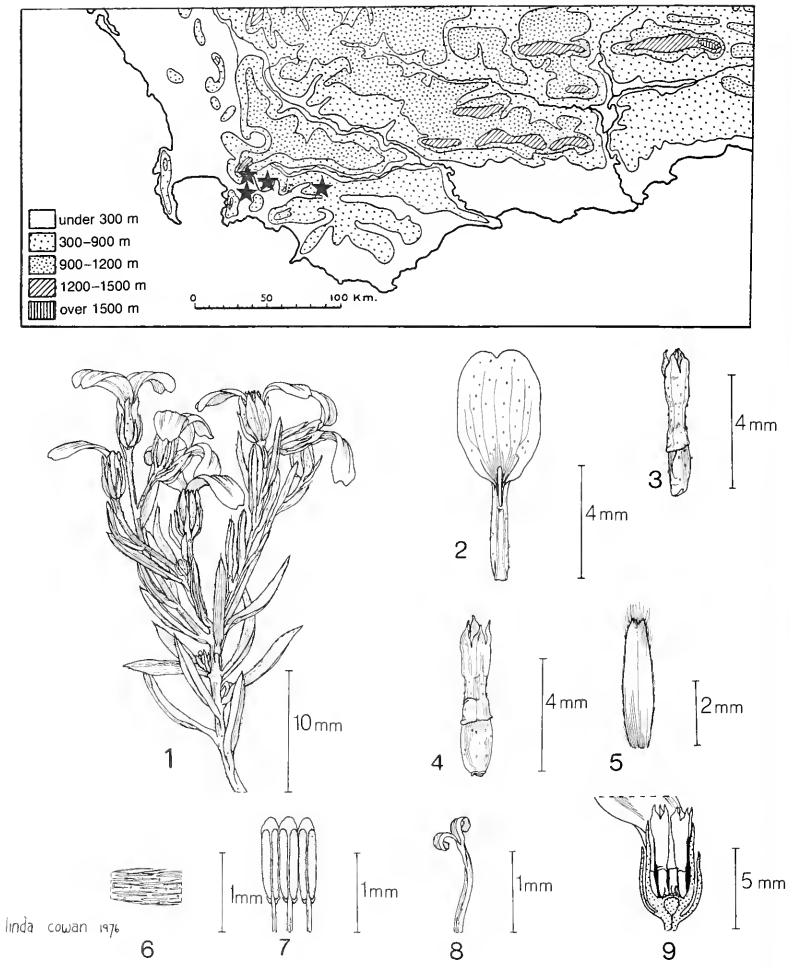

FIG. 3.
Thaminophyllum mundii Harv. (1) Flowering shoot; (2) ray-floret; (3) disc-floret; (4) disc-floret, later stage; (5) inner bract; (6) lower surface of leaf; (7) anthers; (8) upper portion of style and stigma; (9) vertical section through capitulum (stylised). (From *Middlemost 1923*). Distribution map above.

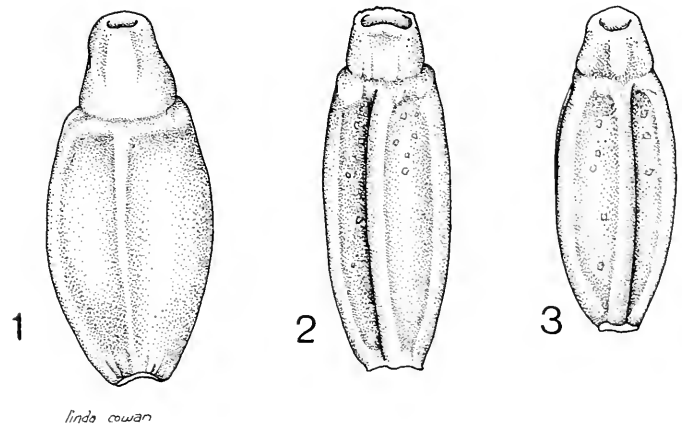

FIG. 4.
Cypselas of (1) *T. latifolium* (2) *T. multiflorum* and (3) *T. mundii* × 15.

anthers 4, 1–1,25 mm long, including the rounded apical appendage; style terete with swollen base, style-branches truncate, stigmatic surface bristly; cypselas oblong, somewhat angled, furnished with a yellowing collar surrounding the stylopodium; pappus 0.

Flowering period: July–November.

Distribution: *T. mundii* occurs in several isolated areas in the Houw Hoek–Elgin mountains and in mountains above Caledon.

Diagnostic characters: This species differs from the other two species in having very few ray-florets (2–4) and in the relative massing of capitula.

SPECIMENS EXAMINED

CAPE—3419 (Caledon): In collibus prope Houw Hoek (-AA), July, *H. Bolus* Herb. No. *384* (BOL, GRA, K, PRE, SAM): in montibus prope Houw Hoek, July, *H. Bolus 5442* (BOL, K, MO, PRE); in rupestribus montium circa Houw Hoek, July, *P. MacOwan 2952* (SAM); Highlands, Elgin, Nov., *A. J. Middlemost 1923* (BOL, NBG, PRE); Zwarteberg (-AB), Oct., *R. Schlechter 5595* (BOL, GRA, PRE); Caledon Wild Flower Show, Sept., *P. Bond 1690* (NBG, PRE); Highlands Forest Reserve (-AC), Oct., *B. Downing 379* (STE); Aug., *P. Bond 1700* (NBG); lower area of Highlands Forest Reserve, Aug., *P. Goldblatt 4771* (K, MO, NBG, PRE, S, US, WAG).

Locality unknown: *Mund s.n.* (K).

ACKNOWLEDGEMENTS

I am grateful to Dr J. P. Rourke, Curator of the Compton Herbarium, for drawing my attention to this attractive little genus in 1976. Dr Rourke's initial impetus and continuing encouragement has been most helpful. I am also indebted to him for photographs of type material. My thanks are gratefully given to Miss Elsie Esterhuysen who unerringly led me to my first sighting of live material of *Thaminophyllum* and also accompanied me on other collecting trips. My thanks to Professor E. A. Schelpe for the latin diagnosis. Miss Linda Cowan's illustrations are a valued contribution. I am indebted to the Directors of all herbaria, whose specimens are cited in this study, for making their collections so freely available to me.

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ACAULESCENT GROWTH FORMS OF *STRELITZIA*: HYBRIDIZATION AND CHROMOSOME NUMBERS

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Abstract

Successful hybridization between *S. reginae* Ait. and *S. juncea* Link was achieved. F_1 plants had intermediate lamina forms. The somatic chromosome complement for parent and F_1 plants was found to be $2n = 14$.

It is speculated that the natural variation in acaulescent growth forms is ecoclinal. Although the junceous form may warrant taxonomic recognition on the basis of its occurrence in pure stands, this study supports the view that the epithet *parvifolia* be abandoned.

Uittreksel

ONGESTINGELDE GROEIVORMS VAN *STRELITZIA*: KRUISING EN CHROMOSOOM GETALLE

Suksesvolle kruisings is tussen *S. reginae* Ait. en *S. juncea* Link gemaak. F_1 plante het intermediêre blaarskyfvorms getoon. Die somatiese chromosoom getal vir beide ouers en F_1 plante is gevind $2n = 14$ te wees.

Daar word gespekuleer dat die natuurlike variasie in blaarvorm wat by die akouliese groeivorms aangetref word ekoklinaal is. Alhoewel die juncea-vorm, weens die voorkoms daarvan in groot suiwer stande, moontlik spesifieke taksonomiese erkenning behoort te geniet, ondersteun hierdie studie die mening dat van die epiteton *parvifolia* afgesien moet word.

Introduction

The genus *Strelitzia* is represented by both caulescent and acaulescent growth forms. Although taxonomists apparently agree on recognizing three caulescent species (*S. nicolai* Regel and Koern, *S. alba* (L.f.) Skeels, *S. caudata* R. A. Dyer) conflicting views on the taxonomic treatment of the acaulescent growth forms have been put forward.

In *Flora Capensis*, Wright (1913) describes two acaulescent species : *S. reginae* and *S. parvifolia*. Moore and Hyypio (1970) suggest that only one species (*S. reginae*) be recognized. Van de Venter, Small & Robbertse (1975) support the suggestion of doing away with the epithet *parvifolia* but together with Dyer (1975) favour the recognition of two species (*S. reginae* Ait. and *S. juncea* Link). *S. reginae* would then include all forms possessing a distinct lamina whereas *S. juncea* would represent the form in which the mature plant either lacks a leaf blade altogether or possesses extremely reduced leaf blades.

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A resolution of this problem would require more information. The present report describes a successful *S. reginae* × *S. juncea* hybridization experiment and provides data from a cytological investigation.

Material and Methods

Hybridization

S. juncea plants (in cultivation. Port Elizabeth) were hand pollinated with *S. reginae* pollen (ex Settler's Park, Port Elizabeth) on September 20, 1974 and inflorescences marked. Only hand-pollinated flowers produced fruits. These were harvested during March 1975.

S. reginae, S. juncea and hybrid seeds were soaked in 4 000 ppm ethrel (Industrial Chemical Products) to break dormancy (Van de Venter and Small, 1975; Van de Venter, 1978) and planted in commercial potting soil contained in 360 mm diameter polythene pots. Seedlings were later thinned to one per pot. In addition to regular watering with tap water, plants received half strength Hoaglands nutrient solution once a week.

During the first year of growth, plants were kept in a growth cabinet (day/night temperature 25/20 °C, 14 h photoperiod) after which they were placed outdoors in full sunlight.

Leaf formation was followed and measurements made on 26 hybrid plants and six each of *S. reginae* and *S. juncea* plants during the period April 1975 to December 1978.

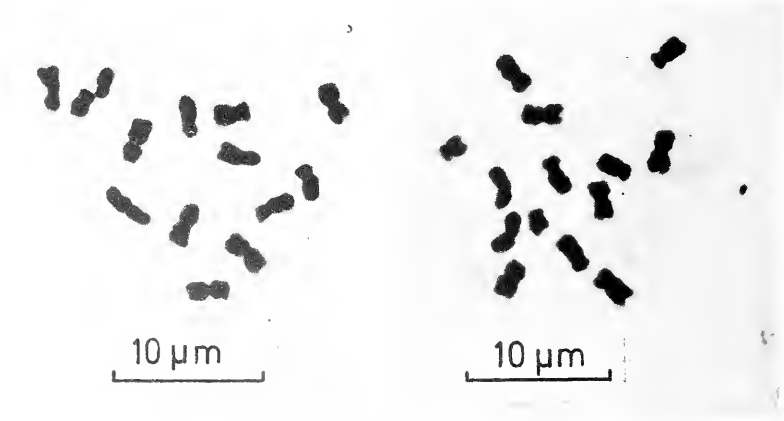

Fig. 1
Somatic chromosomes of (a) *S. reginae* and (b) *S. juncea*

Cytology

Somatic chromosomes were observed in developing anthers of hybrid plants, *S. reginae* and *S. juncea*. Root apices were also examined in the case of the latter two species.

Due to initial difficulties in obtaining good chromosome preparations, a number of fixing and staining techniques were tested. The following procedure gave good results and was followed in this study.

Commencing at 11h00 plant material was pretreated in 4 mM 8-hydroxyquinoline solution for 4 h at 16 °C followed by a 10 min rinse in running tap water. Fixation occurred in an ethanol : acetic acid (3:1) mixture for 1 h at 16 °C. Material was then macerated in ethanol : HCl (2:1) for 16 min at room temperature and then rinsed four times at 15 min intervals with 70% ethanol.

Appropriate pieces of tissue were stained directly on a microscope slide with an aceto-iron-haematoxylin chloral hydrate stain (Wittmann, 1965), squashed, slightly heated and observed in a Carl Zeiss photomicroscope.

Results

Hybridization

Seed obtained from cross-pollinated flowers produced plants which exhibit a distinctly intermediate lamina form between *S. reginae* and *S. juncea*. This was shown clearly by two year old plants (Fig. 1) and is also evident from leaf measurements (Table 1). Note that the differences in leaf measurements between the three groups of plants become increasingly conspicuous as plants become more mature, i.e. with increasing leaf number. It is interesting to note that at this stage of development (leaf 18), petioles of hybrid plants were actually longer than those of either parent plant.

From these results it appears that successful hybridization between *S. reginae* and *S. juncea* was achieved and that the F_1 plants exhibited a reasonably uniform, intermediate lamina form.

Table 1

Leaf measurements at various stages of plant development (mm ± standard deviation)

Leaf No.	Plant type	Lamina length	Lamina width	Petiole length
1.	*S. reginae*	66 ± 8	32 ± 3	42 ± 5
	Hybrids	62 ± 11	34 ± 6	44 ± 9
	S. juncea	55 ± 12	27 ± 5	36 ± 8
9.	*S. reginae*	146 ± 24	79 ± 9	149 ± 39
	Hybrids	125 ± 22	77 ± 14	205 ± 64
	S. juncea	98 ± 7	39 ± 5	181 ± 48
18.	*S. reginae*	281 ± 36	129 ± 5	446 ± 63
	Hybrids	168 ± 39	87 ± 19	649 ± 180
	S. juncea	25 ± 4	5 ± 1	536 ± 140

Chromosomes

Based on a large number of observations the diploid chromosome number for *S. reginae*, *S. juncea* and their hybrid was found to be 14. Morphologically the chromosomes of the three plant groups appeared very similar. Metaphase somatic chromosomes of *S. reginae* and *S. juncea* are shown in Fig. 2.

Discussion

Chromosome numbers in the Strelitziaceae have been published for *S. nicolai* ($2n = 14$), *S. alba* = *S. augusta* ($2n = 22$) and *S. reginae* ($2n = 14$) (Darlington & Wylie, 1955).

The present investigation confirms the $2n = 14$ number for *S. reginae*. It was very interesting to find that *S. juncea* has a somatic chromosome complement equal to that of *S. reginae*. Morphologically the chromosomes of these two species appeared very similar. Further detailed studies would, however, be required to establish similarities or differences in chromosome morphology.

The hybrids in this study resemble some of the intermediate growth forms encountered in the wild at Vensterhoek. Van de Venter *et al.* (1975) postulate that the Vensterhoek plants represent a *S. reginae* × *S. juncea* hybrid population. The present results support this idea. More information is hoped to be gathered from continued crossing studies with our hybrids which have now entered their second flowering cycle.

Fig. 2
Hybrid plant (middle) obtained from crossing *S. reginae* ♂ (left) with *S. juncea* ♀ (right)

The fact that the two extreme acaulescent *Strelitzia* forms hybridize to produce offspring with intermediate lamina forms argues strongly against retaining lamina size as a distinguishing character to delimit acaulescent *Strelitzia* species. It is tempting to speculate that the natural variation encountered is ecoclinal (Heslop-Harrison, 1964).

Although the rather extensive, pure stands of the junceous form at Uitenhage and Port Elizabeth areas may warrant some taxonomic rank for this form, the results of this investigation adds weight to the view of Moore and Hyypio (1970) that only one acaulescent *Strelitzia* species should be recognized. In particular this study has confirmed that the concept of a species with an intermediate sized lamina (*S. parvifolia*) is unacceptable and that this epithet should be abandoned.

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SAADVERSPREIDING VAN ENKELE VERTEENWOORDIGERS VAN DIE MESEMBRYANTHEMACEAE

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UITTREKSEL

'n Verband word aangetoon tussen die saadverspreidingspatroon van 'n spesie en die morfologie van die spesie se kapsule. Strukture soos hokvlerke en plasentale knoppe bevorder ruimtelike saadverspreiding, terwyl die voorkoms van hokvlerke die tempo van saadvrystelling vertraag. By kapsules sonder hokvlerke kan al die sade binne een reënbui vrygestel word, terwyl slegs 'n gedeelte van die sade binne een reënbui vrygestel word by kapsules wat hokvlerke besit. Die voorkoms van saadsakkies in 'n kapsule kan ook die vrystelling van 'n gedeelte van die sade verhoed.

ABSTRACT

SEED DISTRIBUTION OF SOME REPRESENTATIVES OF THE MESEMBRYANTHEMACEAE

The pattern of seed dispersal of a species is correlated to the morphology of the capsule of the species. Structures such as supralocular membranes and placental tubercles improve dispersal in space, whereas the tempo of seed dispersal is lowered by the presence of supralocular membranes. Capsules without these covering membranes can disperse all their seeds during one shower, whereas only a part of the seeds within a capsule is dispersed during a single shower when these membranes are present. Seed pockets can also prevent the dispersal of a part of the seeds within a capsule.

INLEIDING

Verteenwoordigers van die Mesembryanthemaceae kom hoofsaaklik in dorre en woestynagtige gebiede voor. Nie alleen toon die vegetatiewe uitbeelding van hierdie plantsoorte velerlei aanpassings by hul omgewing nie, maar ook ten opsigte van hul saadverspreidingsmeganisme is hierdie plantsoorte by hul dorre habitat aangepas. Feitlik alle lede van die Mesembryanthemaceae besit higrochastiese saadkapsules, dit wil sê die kapsules is in die droë toestand geslote en sodra hulle met water in aanraking kom, voer hulle bewegings uit waardeur die kapsules oopgaan, sodra die kapsules weer uitdroog, gaan hulle weer toe. Saadverspreiding by higrochastiese plantsoorte kan dus slegs tydens reënweer plaasvind, terwyl die sade in 'n droë atmosfeer in die kapsules ingesluit bly. Aangesien saadverspreiding dus vir lang periodes verhinder word, word higrochasie as een van die antitelechoriese saadverspreidingsmeganismes beskou (Zohary, 1937; Van der Pijl, 1972).

Vir publikasie aanvaar 22 Augustus 1979.

Die Bou van die Kapsule van die Mesembryanthemaceae

Die eenvoudigste tipe kapsule bestaan basies uit 'n aantal vrughokke wat deur egte tussenskotte van mekaar geskei word en in die droë toestand aan die bokant deur kleppe bedek word. Die oopgaan van die kapsule in 'n vogtige atmosfeer word deur die kielweefsel veroorsaak wat in die binnekant van die klep geleë is (Fig. 1a–f). Sodra die kielweefsel met water in aanraking kom, swel die selle en veroorsaak dat die kleppe na buite uitgeforseer word (Steinbrinck, 1883; Straka, 1955; Winkler, 1957; Volk, 1961). Wanneer die kleppe oopvou, word daar by sommige spesies dun membraanagtige aanhangsels aan die kleppe gesien wat na buite oopvou en as klepvlerke bekend staan (Fig. 1b, c, d). By sommige genera, byvoorbeeld onder die Aptenioideae, vorm die klepvlerke sakkies wat oor die kleppe lê en nie na buite oopvou nie.

By die meer gevorderde kapsuletipes word gevind dat elke vrughok aan die bokant deur twee hokvlerke bedek word (Fig. 1c-f). Hierdie hokvlerke kan slegs as some aan die rande van die tussenskotte sigbaar wees of hulle kan die vrughokke feitlik volkome aan die bokant bedek. Die buitenste rand van die vrughok, in die omgewing waar die kielweefsel differensieer, word egter nooit deur hokvlerke bedek nie. Hierdie opening van die vrughok word by die gevorderdste tipes deur 'n swelsel van die plasenta, die plasentale knop (Fig. 1d-f), gedeeltelik gevul.

Saadverspreiding

Uit die voorafgaande beskrywing blyk dit dat hoe meer gevorderd die kapsule word, hoe beter is die strukture ontwikkel om die sade in die vrughokke ingesluit te hou selfs nadat die kleppe oopgevou het. Hierdie insluiting van die sade in die kapsules het verskeie navorsers geïnspireer om die meganisme van saadvrystelling na te gaan.

Reeds in 1883 het Steinbrinck op die higrochastiese openingsmeganisme van die kapsules van die Mesembryanthemaceae gewys. Hy meen dat die sade teen die verdorrende invloed van direkte sonstraling beskerm word wanneer hulle in die kapsule ingesluit bly. Hy verkeer egter onder die wanindruk dat die wind die kapsules as 'n geheel versprei. Kerner von Marilaun (1891) noem slegs dat die sade deur reën uit die kapsules gewas word en gee geen verdere verklaring nie. Marloth (1894) beskryf die kapsules van die Mesembryanthemaceae as higrometers: "When the air is damp the flat capsules are closed with a more or less hemispherical top, in the warm sunshine however, the outer tissues of the wall dries and contracts to such an extent that the teeth become quite recurved, forming a pretty star and allowing the seeds to escape from the open capsule when shaken by wind". In werklikheid is dit net die teenoorgestelde wat plaasvind. Hierdie foutiewe opvatting van Marloth (1894) het hy egter later reggestel, onder meer in *The Flora of South Africa* (Marloth, 1913).

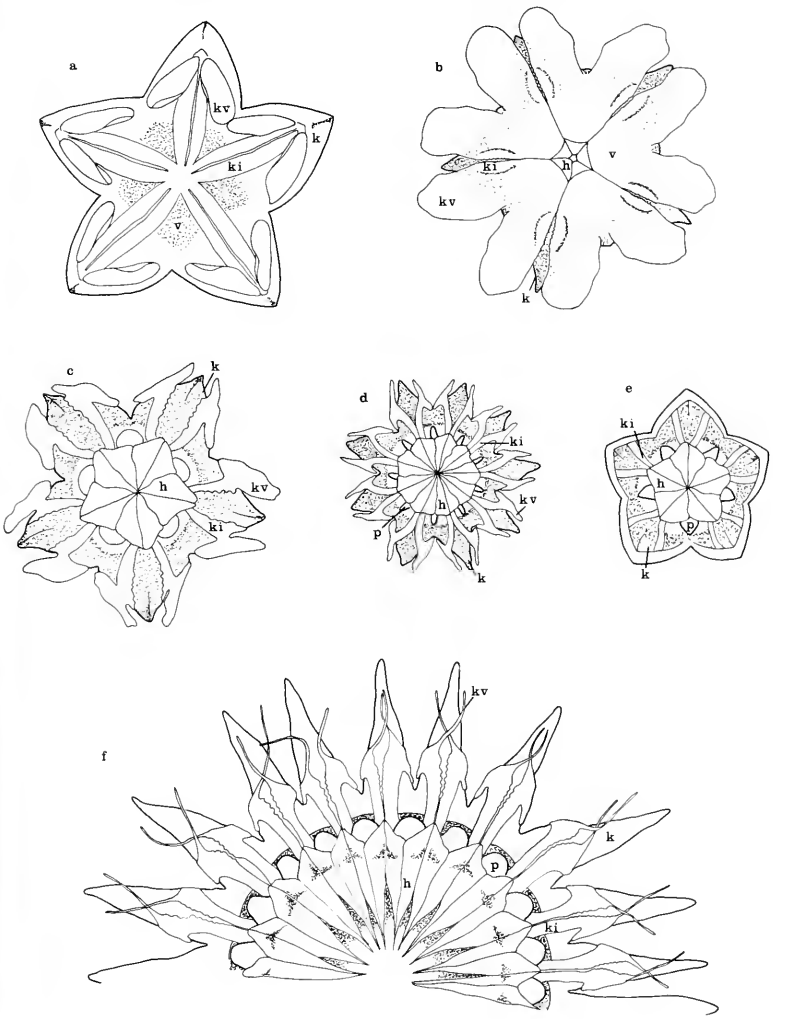

FIG. 1.

'n Bo-aansig van die kapsules van
a. *Mesembryanthemum karrooense*
b. *Micropterum papulosum*
c. *Lampranthus godmaniae*
d. *Polymita albiflora*
e. *Ruschia tribracteata*
f. *Cheiridopsis candidissima*
h = hokvlerk; k = klep; ki = kiel; kv = klepvlerk; p = plasentale knop; v = vrughok

Berger (1908) was die eerste outeur wat met behulp van vallende waterdruppels kon vasstel dat die sade deur reëndruppels uit die kapsules geslinger word. Hy meen dat die eerste paar druppels wat op die vrug val, slegs die vrughokke met water vul sodat die sade net onder die hokvlerke lê. As daar dan 'n verdere reëndruppel op die rand van die vrug val, na aan die uitgang van die vrughok, dit wil sê waar die plasentale knop geleë is, oefen dit 'n druk op die water in die vrughok uit en veroorsaak dat die water in die middel van die hok opwaarts gestoot word en die sade op hierdie manier deur die spleet tussen die hokvlerke geforseer word.

Alhoewel Brown asook Bolus aanvaar dat dit reëndruppels is wat die sade uit die kapsules vrystel, staan hulle skepties teenoor Berger se verklaring van die meganisme (Ihlenfeldt, 1959). Volgens Garside en Lockyer (1930) meen Huber ook dat reëndruppels vir die saadverspreiding verantwoordelik is maar glo nie dat die reëndruppels die sade direk uit die kapsules by tipes met hokvlerke kan uitslinger nie.

In 1930 het Garside en Lockyer die resultate van 'n reeks proewe met kapsules van *Carpanthea pomeridiana* gepubliseer. Hulle kon bewys dat die vallende waterdruppel op die buitenste rand van die kapsule moes val om doeltreffend te wees en dat die sade in die middel van die kapsule vrykom en dan oor die kapsule geskiet word. Verder beweer Garside en Lockyer (1930) dat strukture soos hokvlerke nie veroorsaak dat die sade binne een kapsule geleidelik in opeenvolgende reënbuie uitgestrooi word nie.

Lockyer het in 1932 sy verdere bevindings in verband met die saadverspreiding van die Mesembryanthemaceae gepubliseer. Hierdie keer het hy met die kapsules van *Bergeranthus scapigerus* en *Dorotheanthus bellidiformis*, wat albei goed ontwikkelde hokvlerke besit, geëksperimenteer. In die een geval het hy die hokvlerke uitgedissekteer en gevind dat wanneer waterdruppels op so 'n kapsule val, die saad nie so ver vanaf die kapsule beland as wanneer die hokvlerke aanwesig is nie, maar dat die tempo van saadvrystelling hoër is wanneer die hokvlerke verwyder is. Weer eens beklemtoon Lockyer egter sy mening dat die hokvlerke nie verhoed dat al die sade van een kapsule binne een reënbui vrygelaat word nie.

Volk (1961) het soortgelyke eksperimente uitgevoer waar hy die uitstrooiing van die sade vergelyk het by:

a. kapsules sonder hokvlerke of plasentale knoppe;
b. kapsules met hokvlerke sonder plasentale knoppe en
c. kapsules met hokvlerke en plasentale knoppe.

Sy bevindings dui daarop dat die afstande wat die sade van die kapsule uitgestrooi word, van groep a na c toeneem, terwyl die tempo van vrystelling van groep a na c afneem.

In die huidige studie is eerstens die afstande van uitstrooiing asook die tempo van uitstrooiing by ses verskillende spesies ondersoek. Hierdie ses spesies vorm 'n

reeks vanaf spesies met primitiewe soorte kapsules wat geen hokvlerke of plasentale knoppe besit nie, na die spesies met kapsules waar albei hierdie strukture voorkom. Die organografiese uitbeelding van die sade van die ses verskillende spesies is ook nagegaan vir 'n moontlike verband tussen saadvorm en afstand van uitstrooiing.

In die tweede reeks eksperimente is die saadverspreiding van *Cheiridopsis candidissima* vergelyk tussen:

a. ''normale'' kapsules waar beide die hokvlerke en plasentale knoppe nog aanwesig was,
b. kapsules waarvan slegs die plasentale knoppe verwyder was en
c. kapsules waarvan slegs die hokvlerke verwyder was.

Materiaal en Metode

Die kapsules en saad van al ses spesies wat ondersoek is, is op die Hester Malan-natuurreservaat naby Springbok in Namakwaland (Rösch, 1977) versamel. Die oppervlakke van die sade is met behulp van 'n aftaselektronmikroskoop ondersoek.

Vir die bepaling van die afstande waaroor die saad uit 'n kapsule geslinger is, is die vloer van die laboratorium met 'n 4 × 4 m stuk wit papier bedek. Konsentriese sirkels met 0,2 m intervalle is om die middelpunt van die papier getrek. Die basis van 'n oop kapsule is in 'n stuk speelkraamklei geplaas sodat die boonste oppervlak van die kapsule so na as moontlik horisontaal georiënteer was en die klei plus kapsule is by die middelpunt van die konsentriese sirkels geplaas. 'n Mediese binne-aarse drupapparaat (Plexitron R41) met 'n 0,8 × 38 naald aan die punt van die drupbuis is so opgestel dat die druppels van 'n hoogte van 2 m teen 'n tempo van 90 per minuut op die oop kapsule geval het. Die gemiddelde massa van 'n druppel was naastenby 12,5 mg en die gemiddelde deursnee was naastenby 2,88 mm. 'n Oop kapsule is eerstens vir vyf minute onder die vallende druppels geplaas waarna die eksperiment gestaak is. Die posisies waarheen die sade uitgestrooi was, is aangeteken en daarna is die sade van die papier verwyder. Die proses is vir 'n verdere vyf minute herhaal, daarna weer vir 20 minute en laastens vir twee en 'n half uur wat 'n totaal van drie uur blootstellingstyd gegee het. Daarna is die aantal sade wat nog in die kapsule oorgebly het, getel. Ten minste twee herhalings is vir elke spesie gebruik, maar afhangende van die aantal sade per kapsule is 'n verskillende aantal kapsules per spesie ondersoek om 'n minimum van 50 sade wat uitgestrooi is, te verkry.

In die tweede reeks eksperimente waar verskillende kapsules van *Cheiridopsis candidissima* vergelyk is, is konsentriese sirkels met 0,1 m intervalle rondom die kapsules getrek en die aantal sade binne elke konsentriese sone is na vyf minute, 'n verdere vyf minute en 'n verdere 20 minute (totaal 30 minute blootstellingstyd) getel. Eerstens is die ongewysigde kapsules van *Cheiridopsis candidissima* geneem, daarna is kapsules geneem waarvan die plasentale knoppe uitgedissekteer

TABEL 1
Kenmerke van die kapsules van ses verskillende spesies wat ten opsigte van saadverspreiding vergelyk is

	Mesembryanthemum karrooense	*Micropterum papulosum*	*Lampranthus godmaniae*	*Polymita albiflora*	*Ruschia tribracteata*	*Cheiridopsis candidissima*
Aantal vrughokke	5	5	5	8–10	5	16–20
Hokvlerke	Afwesig	Klein	Aanwesig	Aanwesig	Aanwesig	Aanwesig
Plasentale knoppe	Afwesig	Afwesig	Afwesig	Aanwesig	Aanwesig	Aanwesig
Saadsakkies	Afwesig	Swak ontwikkel	Afwesig	Afwesig	Afwesig	Afwesig

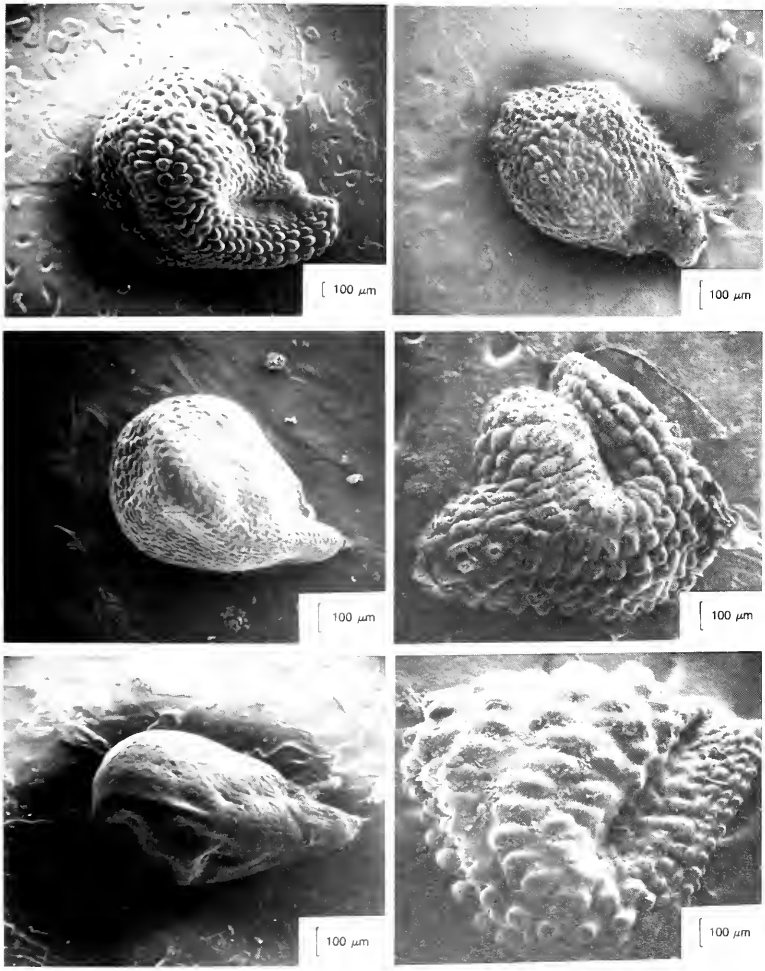

FIG. 2.
Oppervlakaansig van die sade van
a. *Mesembryanthemum karrooense*
b. *Micropterum papulosum*
c. *Lampranthus godmaniae*
d. *Polymita albiflora*
e. *Ruschia tribracteata*
f. *Cheiridopsis candidissima*

was en derdens is kapsules waarvan die hokvlerke uitgedissekteer was, ondersoek. In elke geval is daar drie herhalings gedoen.

Resultate en Bespreking

Die hoofkenmerke van die kapsules wat vergelyk is, word in Tabel 1 opgesom. In Figuur 2 word 'n aftaselektronmikrograaf van die saad van elk van die spesies afgebeeld. In Figuur 3 word die persentasies sade wat in verskillende konsentriese sones vanaf die kapsules te lande gekom het as histogramme aangegee. Hierdie waardes is as persentasies van die totale aantal sade wat die kapsule verlaat het, bereken. Verder word daar in Figuur 4 aangetoon watter persentasie van die totale aantal sade wat oorspronklik in die kapsule was, na die verskillende tydsintervalle nog in die kapsule oor was.

Mesembryanthemum karrooense

Van al die ondersoekte soorte, is die kapsules van *Mesembryanthemum karrooense* (Fig. 1a) die eenvoudigste. Dit bestaan uit vyf relatief smal, diep vrughokke en is die enigste van die ses ondersoekte soorte met aksiale plasentasie. Die kiele lê langs mekaar in die middel van elke klep. Geen hokvlerke kom voor nie maar goed ontwikkelde klepvlerke wat oor die kleppe lê en sakkies vorm, is teenwoordig. Die sade van *M. karrooense* is naastenby D-vormig en het 'n baie growwe oppervlak (Fig. 2a) en besit 'n gemiddelde massa van 0,22 mg.

Die eksperimentele resultate (Fig. 3a) toon aan dat die grootste persentasie (55,12%) van die sade binne die eerste 0,2 m vanaf die kapsule te lande gekom het en dat 90,29% van die vrygestelde sade binne 0,6 m van die kapsule beland het. Die afstand wat die verste saad vanaf die kapsule bereik het, was 1,26 m. Binne die eerste vyf minute van die eksperiment is die grootste persentasie (78,22%; Fig. 4a) van die sade vrygestel en na afloop van die drie uur het geen sade in die kapsules oorgebly nie.

Micropterum papulosum

In 'n bo-aansig het die oop kapsule van *Micropterum papulosum* (Fig. 1b) ook 'n baie primitiewe struktuur. Die kapsule bestaan uit vyf vrughokke wat slegs in die sentrale gedeelte deur swak ontwikkelde hokvlerke bedek word. Die plasentasie is parietaal en geen plasentale knoppe kom voor nie. Die twee kiele aan die binnekant van elke klep verloop feitlik ewewydig aan mekaar en aan elke klep kom twee groot klepvlerke voor. In 'n lengtesnee deur 'n kapsule van *M. papulosum* word egter gevind dat die kapsule nie so primitief is nie aangesien swak ontwikkelde saadsakkies (Ihlenfeldt, 1959) voorkom. Aan die basis van elke vrughok word naamlik 'n sogenaamde plasentale tussenskot gevorm waardeur die plasenta gelig word. Alhoewel die holtes wat sodoende aan weerskante van die plasentale tussenskot gevorm word, nie volkome van die res van die vrughok

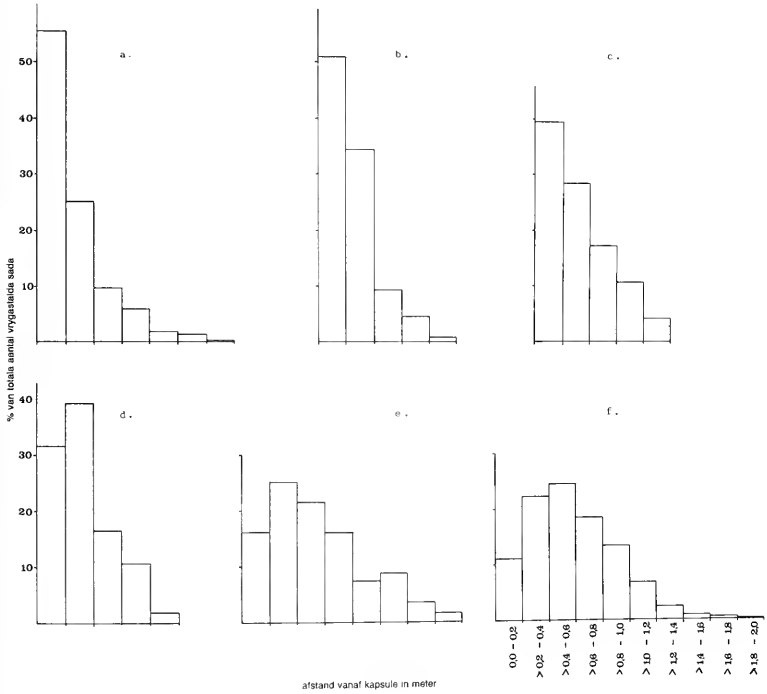

FIG. 3.
Persentasies van die vrygestelde sade wat in 0,2 m konsentriese sones vanaf die kapsule beland het as gevolg van vrystelling deur vallende waterdruppels, by
a. *Mesembryanthemum karrooense*
b. *Micropterum papulosum*
c. *Lampranthus godmaniae*
d. *Polymita albiflora*
e. *Ruschia tribracteata*
f. *Cheiridopsis candidissima*

afgegrens is nie, is die plasenta aan die bokant effens geswel sodat die opening van die holte vernou is. Normaalweg ontwikkel daar een tot twee sade in elk van hierdie saadsakkies. Die opening aan die bokant van hierdie saadsakkies is egter nog steeds groot genoeg vir 'n saad om daardeur te ontsnap na die hoofholte van die vrughok sodat daar geen sprake van egte paraspermie (Schwantes, 1952) is nie. Die vorm van die sade van *M. papulosum* is ook naastenby D-vormig (Fig. 2b) maar die oppervlak van die sade is minder grof as dié van *Mesembryanthemum karrooense*. Die gemiddelde massa van die sade van *Micropterum papulosum* is 0,60 mg.

Wanneer die eksperimentele resultate (Fig. 3b) van *Micropterum papulosum* nagegaan word, word gevind dat die grootste persentasie (50,79 %) van die sade wat uitgeskiet is, binne 0,2 m vanaf die kapsule geval het. Slegs 5,55 % van die sade wat uitgeskiet is, het verder as 0,6 m vanaf die kapsule te lande gekom met die verste saad 0,94 m vanaf die kapsule.

Die tempo van saadvrystelling tydens die duur van die eksperiment (Fig. 4a) toon aan dat die grootste persentasie van die oorspronklike aantal sade in die kapsule (50,80 %), tydens die eerste vyf minute van die eksperiment vrygestel is. Opvallend is egter die redelike hoë persentasie (32,62 %) van die oorspronklike aantal sade in die kapsule, wat na afloop van die eksperiment nog in die kapsule agtergebly het.

Lampranthus godmaniae

Die kapsule van *Lampranthus godmaniae* (Fig. 1c) is vyfhokkig en elke vrughok word aan die bokant deur goed-ontwikkelde hokvlerke bedek. Wanneer die kleppe oopgaan, kan die twee kiele wat van mekaar divergeer aan die binnekant van elke klep waargeneem word asook die duidelike klepvlerke wat dan uitsprei. Geen plasentale knoppe kom voor nie, maar die funikulusse aan die buitenste rand van die plasenta vorm 'n digte ineengestrengelde massa wat tot 'n mate die buitenste opening van die vrughok versper. By *L. godmaniae* word dus gevind dat selfs al is die kleppe van die kapsule oopgevou, lê die sade nie direk aan die omgewing blootgestel nie, maar die sade word nog steeds deur die hokvlerke bedek. Die sade van *L. godmaniae* is D-vormig, het 'n onegalige oppervlak (Fig. 2c) en besit 'n gemiddelde massa van 1,05 mg.

Alhoewel die grootste persentasie (39,13 %) van die sade wat in verskillende konsentriese sones beland by *L. godmaniae* nog steeds binne 0,2 m vanaf die kapsule val, is die afname in die aantal sade wat verder vanaf die kapsule beland meer geleidelik as by die eerste twee ondersoekte kapsuletipes (Fig. 3c). Die grootste afstand wat 'n saad vanaf die kapsule afgelê het, was 0,97 m. By *L. godmaniae* is die persentasie sade wat binne die eerste vyf minute vrygestel is nog steeds die grootste (63,04 %) en na 30 minute was daar geen sade in die kapsules oor nie (Fig. 4a).

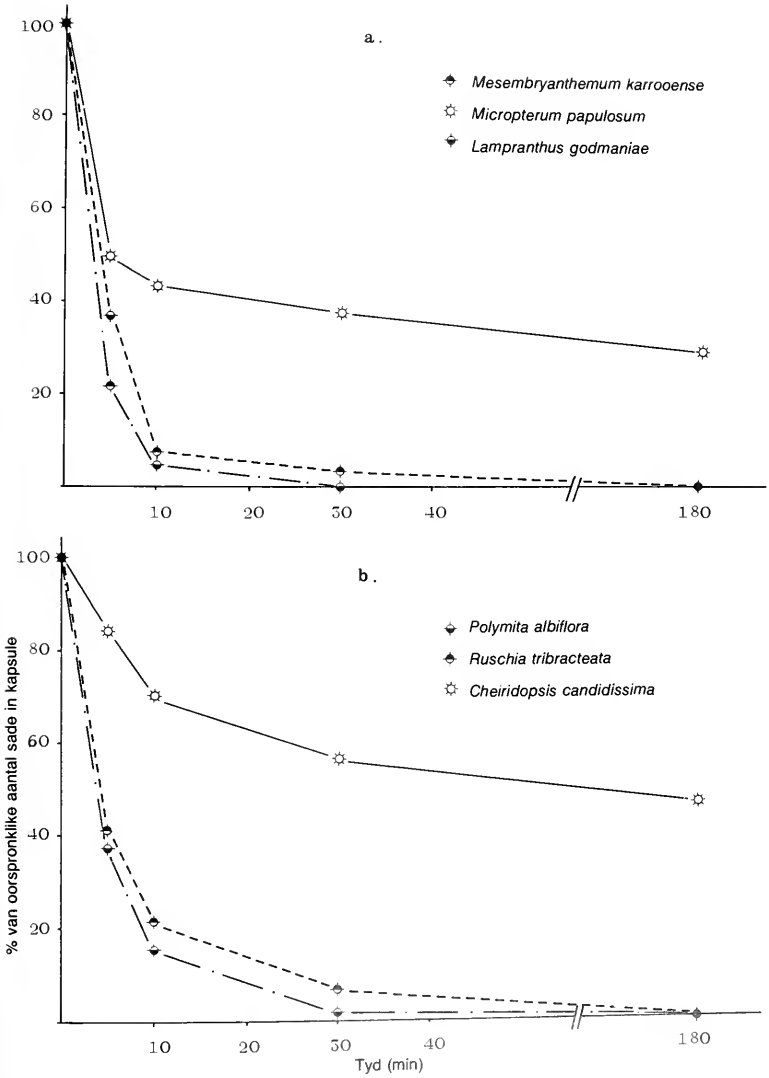

FIG. 4.

Persentasies van die oorspronklike aantal sade in 'n kapsule wat nog in die kapsule oorbly na verskillende tye van blootstelling aan vallende waterdruppels, by

a. *Mesembryanthemum karrooense; Micropterum papulosum* en *Lampranthus godmaniae*
b. *Polymita albiflora; Ruschia tribracteata* en *Cheiridopsis candidissima*

Polymita albiflora

By *Polymita albiflora* (Fig. 1d) wissel die aantal vrughokke van agt tot tien per kapsule. Die sentrale gedeelte van elke vrughok word deur hokvlerke bedek en die opening aan die buitenste rand van die vrughok word deur die plasentale knop versper. Aan die binnekant van elke klep loop die kiele gedeeltelik ewewydig aan mekaar en divergeer dan skielik van mekaar. Duidelike klepvlerke kan aan die kleppe waargeneem word. Die sade is peervormig met 'n effens geriffelde oppervlak (Fig. 2d) en besit 'n gemiddelde massa van 0,11 mg. Hierdie sade word in die vrughokke ingesluit deur die hokvlerke asook die plasentale knoppe en lê dus selfs wanneer die klepvlerke oopvou, nie aan die omgewing blootgestel nie.

'n Ondersoek van die eksperimentele resultate (Fig. 3d en 4b) van *Polymita albiflora* toon aan dat die grootste persentasie (39,13 %) van die sade wat in 'n 0,2 m konsentriese sone beland het, nie meer binne 0,2 m vanaf die kapsule geval het nie maar wel van > 0,2 m tot 0,4 m vanaf die kapsule. Die afstand wat die verste saad vanaf die kapsule bereik het, was 0,99 m. Die tempo van saadvrystelling was nog die hoogste binne die eerste vyf minute van die eksperiment toe 63,35 % van die totale aantal sade vrygestel is. Ten spyte daarvan dat 'n groter persentasie van die sade vir 'n langer tyd in die kapsule teruggehou is as by *Lampranthus godmaniae* en *Mesembryanthemum karrooense*, het daar geen sade na afloop van die eksperiment (drie uur) in die kapsule oorgebly nie.

Ruschia tribracteata

Die kapsule van *Ruschia tribracteata* (Fig. 1e) stem baie met dié van *Polymita albiflora* ooreen. Elkeen van die vyf vrughokke word in die sentrale gedeelte deur hokvlerke bedek en die opening van die vrughok aan die buitenste rand word deur goed-ontwikkelde, naastenby driehoekige plasentale knoppe versper. Die kiele aan die binnekant van die kleppe divergeer van mekaar en geen klepvlerke kom voor nie. Die sade is naastenby peervormig en besit 'n onegalige oppervlak (Fig. 2e). Die massa van die sade is gemiddeld 0,12 mg.

In die geval van *Ruschia tribracteata* is gevind (soos by *Polymita albiflora)* dat die grootste persentasie (25,00 %) van die sade wat in 'n 0,2 m konsentriese sone beland het, van > 0,2 tot 0,4 m vanaf die kapsule te lande gekom het, maar dat 'n aansienlike persentasie (21,43 %) van die sade van > 0,4 tot 0,6 m vanaf die kapsule beland het (Fig. 3e). By *R. tribracteata* het altesame 14,29 % van die sade verder as 1 m vanaf die kapsule te lande gekom en die verste saad is 1,41 m vanaf die kapsule gevind. Wanneer die tempo van saadvrystelling by *R. tribracteata* nagegaan word, word opgemerk dat die sade meer geleidelik uit die kapsule vrygestel is as in die vorige gevalle (Fig. 4b). Nogtans is gevind dat die kapsules na afloop van die eksperiment nie meer sade bevat het nie.

Cheiridopsis candidissima

Die kapsules van *Cheiridopsis candidissima* (Fig. 1f) kan as 'n veelhokkige variasie van dié van *Ruschia tribracteata* beskou word. By die kapsules van *C. candidissima* kom van 16 tot 20 vrughokke voor. Aan die bokant van elke vrughok kom die hokvlerke voor wat effens na buite uitgestulp is. Die opening aan die buitenste rand van elke vrughok word deur 'n groot plasentale knop versper. Aan die binnekant van elke klep verloop die kiele gedeeltelik ewewydig aan mekaar en wyk dan van mekaar uit. Elke kiel loop uit in 'n naaldvormige klepvlerk. Die sade van *C. candidissima* is naastenby peervormig met 'n gladde oppervlak (Fig. 2f) en besit 'n gemiddelde massa van 0,17 mg.

By *Cheiridopsis candidissima* is gevind (Fig. 3f) dat die grootste persentasie (24,64 %) van die sade wat in 'n 0,2 m konsentriese sone beland het, van > 0,4 tot 0,6 m vanaf die kapsule beland het en dat die persentasie sade wat binne die eerste 0,2 m vanaf die kapsule te lande gekom het, relatief laag was. Die afstand wat die verste saad van *C. candidissima* vanaf die kapsule afgelê het, was 1,98 m. Dit is die grootste afstand wat by enige van die ondersoekte soorte aangetref is. Die tempo waarteen die sade by *C. candidissima* vrygestel is, was heelwat laer as by die voorafgaande gevalle en na afloop van die eksperiment was daar nog 47,79 % van die oorspronklike aantal sade in die kapsule oor (Fig. 4b).

Higrochasie word as een van die antitelechoriese saadverspreidingsmeganismes beskou waar die verhindering van saadverspreiding veral ten opsigte van tyd plaasvind (Zohary, 1937, 1962; Sohary & Fahn, 1941; Van der Pijl, 1972). By die Mesembryanthemaceae blyk dit egter asof meganismes om saadverspreiding te bevorder en te verhinder dikwels by dieselfde plantsoort aanwesig is. By die primitiewe kapsuletipes, byvoorbeeld *Mesembryanthemum karrooense,* is gevind dat die grootste persentasie van die sade direk om die kapsule versprei is, maar die meeste sade is binne 'n baie kort tydperk uit die kapsule vrygestel. Alhoewel die saad by hierdie soorte ook slegs tydens 'n reënbui versprei kan word, is dit moontlik dat al die sade van een kapsule binne 'n enkele reënbui versprei kan word. Namate die kapsules meer gevorderd raak en hokvlerke en plasentale knoppe voorkom, byvoorbeeld by *Polymita albiflora, Ruschia tribracteata* en *Cheiridopsis candidissima*, verander die saadverspreidingspatroon heeltemal. Alhoewel hierdie plantsoorte nog steeds antitelechories is, verhoog strukture soos hokvlerke en plasentale knoppe waarskynlik die afstande waaroor saadverspreiding plaasvind. Aan die ander kant verlaag die voorkoms van hierdie strukture die tempo waarteen die sade uit die kapsule vrygestel word. Dit is dus onwaarskynlik dat hierdie kapsules tydens een reënbui al hulle sade sal vrystel.

Lockyer (1932) het reeds aangetoon dat nadat die hokvlerke van die kapsules van *Bergeranthus scapigerus* sowel as van *Dorotheanthus bellidiformis* verwyder is, die sade nie meer so ver vanaf die kapsule deur vallende waterdruppels uitgestrooi word as wanneer die hokvlerke nog teenwoordig is nie. Alhoewel daar dikwels beweer word (Ihlenfeldt, 1971; Volk, 1961) dat die plasentale knoppe in

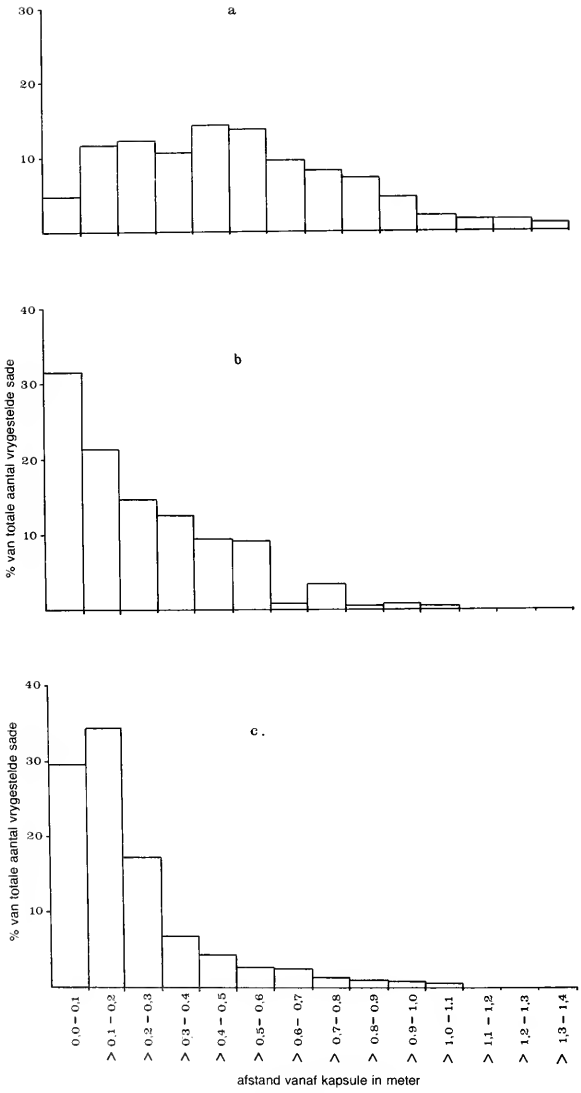

FIG. 5.

Persentasies van die vrygestelde sade wat in 0,1 m konsentriese sones vanaf die kapsules van *Cheiridopsis candidissima* beland, by

a. "normale kapsule"
b. kapsule sonder plasentale knoppe en
c. kapsule sonder hokvlerke

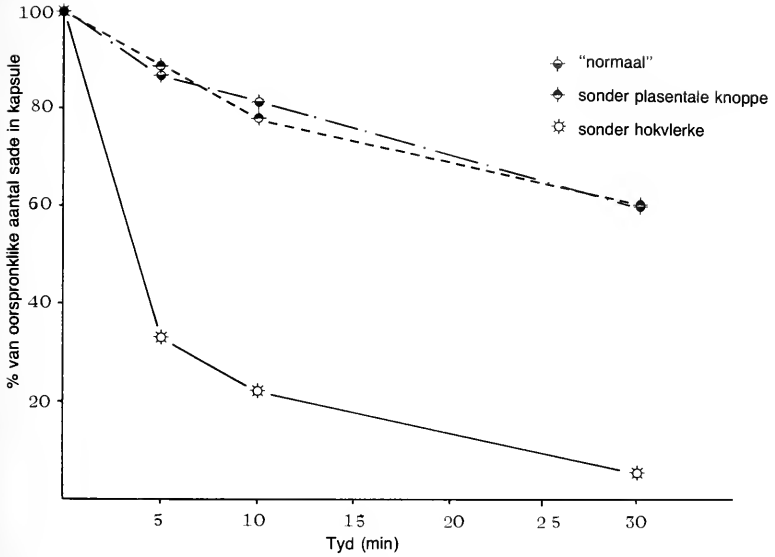

FIG. 6.
Persentasies van die oorspronklike aantal sade in 'n kapsule wat nog in die kapsules van *Cheiridopsis candidissima* oorbly na verskillende tye van blootstelling aan vallende waterdruppels, by
"normale kapsule"
kapsule sonder plasentale knoppe en
kapsule sonder hokvlerke

hierdie opsig dieselfde funksie as die hokvlerke verrig, is daar geen direkte eksperimentele gegewens om hierdie bewering te staaf nie. Kapsules van *Cheiridopsis candidissima* is derhalwe geneem en in hierdie opsig ondersoek.

In die geval van die "normale kapsule" van *Cheiridopsis candidissima* het die grootste persentasie van die vrygestelde sade (14,21 %; Fig. 5a) wat in enige van die konsentriese sones beland het van > 0,5 tot 0,6 m vanaf die kapsule te lande gekom. Die verste saad het in die > 1,3 tot 1,4 m sone beland. Gedurende die hele uitspattingsperiode is in totaal 39,29 % (Fig. 6) van die sade uit die kapsules vrygestel.

By kapsules van *Cheiridopsis candidissima* waarvan die plasentale knoppe verwyder is, is gevind dat die grootste persentasie van die vrygestelde sade (31,68 %; Fig. 5b) binne 0,1 m vanaf die kapsule te lande gekom het en meer as die helfte van die sade wat vrygestel is (52,80 %), het binne 0,2 m vanaf die kapsule beland. Die afstand wat die verste saad vanaf die kapsule bereik het, was

nie meer as 1,1 m nie. In totaal is 39,19% (Fig. 6) van die oorspronklike aantal sade in die kapsule vrygestel.

In die geval waar die hokvlerke verwyder was, is gevind dat die grootste persentasie van die vrygestelde sade (34,45%; Fig. 5c) wat in enige van die konsentriese sones beland het, tussen > 0,1 en 0,2 m vanaf die kapsule te lande gekom het en altesame 64,15% van die sade wat vrygestel was, het binne 0,2 m vanaf die kapsule beland. Die persentasie van die oorspronklike aantal sade wat vrygestel is, was 98,68% en 66,22% van die oorspronklike aantal sade is binne die eerste vyf minute vrygestel (Fig. 6).

Hierdie resultate demonstreer dus duidelik dat die aanwesigheid van die plasentale knoppe sowel as die hokvlerke 'n toename in die afstand wat die sade vanaf die kapsule versprei word, teweegbring. Ten spyte daarvan dat die persentasie sade wat binne die verskillende tydsintervalle vrygestel is by die "normale kapsule" en dié waar die plasentale knoppe verwyder is, effens verskil het, het daar na die 30 minute blootstellingstyd bykans dieselfde persentasie van die oorspronklike aantal sade in die kapsules oorgebly. Die plasentale knoppe dra dus waarskynlik nie wesenlik daartoe by dat die sade vir 'n langer tyd in die kapsules ingesluit bly nie. In teenstelling hiermee dui die resultate van die kapsules waar die hokvlerke verwyder is aan dat die tempo van saadvrystelling grootliks deur die aanwesigheid van hokvlerke vertraag word.

Garside en Lockyer beweer in 1930 dat hulle van mening is dat die hokvlerke nie sal verhoed dat al die sade binne 'n enkele reënbui uit 'n kapsule vrygelaat word nie. In 1932 beklemtoon Lockyer hierdie bewering: "That the wings are a device for preventing all the seeds from becoming dispersed in one shower I do not believe. Experimentally a capsule has been emptied (except for 8 seeds) in ten minutes when the drops were falling at the rate of forty per half-minute, so that a heavy storm of rain should accomplish the same result in much less time". In die eksperiment waarna Lockyer (1932) verwys, het hy met 'n kapsule van *Bergeranthus scapigerus* geëksperimenteer en het die waterdruppels wat op die kapsule geval het 'n radius van 2,69 mm gehad. Wat hierdie outeurs egter skynbaar nie in ag geneem het nie was dat die intensiteit van die waterdruppels wat hulle tydens die eksperiment gebruik het, baie hoër was as wat normaalweg, selfs tydens 'n swaar donderstorm, in die natuur ondervind word. So kan bereken word dat indien daar vir tien minute lank, 80 druppels per minuut val, soos wat tydens Lockyer se eksperiment die geval was, is die volume van hierdie druppels naastenby 65 228 mm^3. Al hierdie druppels het tydens die eksperiment op naastenby dieselfde plek geval. Gestel die oppervlakte waarop die druppels geval het, was 100 mm^2 dan sal die 800 waterdruppels gelykstaande aan 'n reënbui van 652 mm wees. Hierdie syfer is vier keer die reënvalsyfer wat 'n gebied soos die Namakwalandse Gebroke Veld, waar baie van die Mesembryanthemaceae voorkom, gemiddeld in een jaar ontvang. Die hoeveelheid reën wat dus benodig word om al die sade uit die kapsule van *Bergeranthus scapigerus* vry te stel, is dus meer as wat normaalweg

binne 'n enkele reënbui val. Gevolglik sal daar normaalweg slegs 'n gedeelte van die sade van 'n kapsule met hokvlerke binne 'n enkele reënbui vrygestel word.

Nie alleen was die intensiteit van die waterdruppels wat Lockyer (1932) tydens sy eksperiment gebruik het, baie hoër as wat normaalweg ondervind word nie, maar die grootte van die waterdruppels was ook baie groter as dié van normale reëndruppels. Volgens Saville en Hayhoe (1978) breek groot reëndruppels naamlik tydens hul val uiteindelik op in druppels met 'n deursnee van minder as 2,2 mm. Hulle beweer dat 'n waterdruppel met 'n deursnee van 4 mm binne 0,5 m se vrye val 'n snelheid van 3 $m.s^{-1}$ bereik en dat daardie druppel reeds feitlik twee maal soveel momentum besit as 'n druppel met 'n deursnee van 2,5 mm wat grenssnelheid bereik het. Aangesien Lockyer (1932) tydens sy eksperiment van druppels met 'n deursnee van 5,38 mm gebruik gemaak het, was die momentum van daardie druppels nadat hulle deur 1,75 m geval het (soos in sy eksperimente) baie groter as dié van die meeste reëndruppels. 'n Groot persentasie van die Mesembryanthemaceae kom in winterreënvalstreke voor waar swaar donderstorms selde ondervind word en die reën gewoonlik sag is. Hierdie inligting maak dit dus in 'n verdere opsig onwaarskynlik dat die sade van een kapsule, wat hokvlerke besit, binne 'n enkele reënbui vrygestel sal kan word.

Die kapsule van *Micropterum papulosum* is in sekere opsigte relatief primitief en in ander opsigte weer relatief gevorderd. Waarskynlik as gevolg van die afwesigheid van hokvlerke en plasentale knoppe word gevind dat die sade nie baie ver vanaf die kapsule uitgestrooi word nie. Die voorkoms van saadsakkies by *M. papulosum* is egter 'n gevorderde kenmerk (Schwantes, 1952). Alhoewel die saadsakkies by hierdie spesie nog swak ontwikkel is en die sade nie volkome in die saadsakkies ingesluit word nie is die saadsakkies in staat om 'n sekere persentasie van die sade in die kapsule terug te hou.

Daar kan 'n verband aangetoon word tussen die vorm en oppervlakskulptuur van die saad van 'n spesie aan die een kant en die gemiddelde afstand van saadverspreiding van 'n spesie aan die ander kant. By die soorte waar die grootste persentasie van die sade binne 0,2 m vanaf die kapsule te lande gekom het (Fig. 3a, b en c), naamlik *Mesembryanthemum karrooense*, *Micropterum papulosum* en *Lampranthus godmaniae* is die sade min of meer D-vormig, terwyl die oppervlak van die sade baie onreëlmatig is (Fig. 2a, b en c). By die groep waar die grootste persentasie van die sade verder as 0,2 m vanaf die kapsule te lande gekom het (Fig. 3d, e en f), naamlik *Polymita albiflora*, *Ruschia tribracteata* en *Cheiridopsis candidissima* is die sade min of meer peervormig en die oppervlak redelik glad (Fig. 2d, e en f). Alhoewel die massas van laasgenoemde drie spesies se sade kleiner as dié van eersgenoemde drie spesies se sade is, is daar geen direkte verband tussen die gemiddelde massa van 'n spesie se saad en die afstand van verspreiding nie. Naas die vorm en massa van sade, kan aanvaar word dat die geometrie van die vrughokke ook 'n belangrike invloed op die afstand waarheen sade uitgestrooi word, moet uitoefen.

Die afstand wat die verste saad in hierdie eksperimente vanaf die kapsule te lande gekom het, kan nie as die verspreidingsgrens van die spesie in die natuur beskou word nie. In hierdie eksperimente het die waterdruppels 'n deursnee van 2,9 mm gehad. Nadat hierdie druppels 2 m geval het, het die druppels nog nie hulle grenssnelheid bereik nie, met die gevolg dat 'n druppel van dieselfde grootte in die natuur waarskynlik 'n groter momentum het wanneer dit die kapsule tref en die sade sal dus waarskynlik verder deur so 'n druppel uitgestrooi word. Volgens Saville en Hayhoe (1978) het die meeste reëndruppels egter 'n deursnee van minder as 2,2 mm wanneer hulle die aarde tref. In die natuur word die snelheid van vallende reëndruppels egter dikwels deur turbulensie vertraag sodat die druppels nie noodwendig hul grenssnelheid bereik het wanneer hulle die kapsule tref nie. Wind veroorsaak ook dikwels dat die druppels skuins val waardeur die doeltreffendheid van die reëndruppels verlaag (of soms moontlik verhoog) kan word (Saville & Hayhoe, 1978).

Wanneer hierdie eksperimenteel-verkreë waardes met toestande in die veld vergelyk word, moet die hoogte waarop die kapsules gedra word ook in ag geneem word. By *Micropterum papulosum* word die kapsules byvoorbeeld plat teen die grondoppervlak gedra, terwyl die kapsules van *Polymita albiflora* van 0,1 tot 0,3 m hoog gedra word. 'n Toename in hoogte van die kapsule vanaf die grondvlak sal daartoe bydra dat die sade verder uit die kapsule gestrooi word.

Higrochasie is 'n seldsame verskynsel in die planteryk en is tot die dorre wêrelddele beperk (Zohary, 1937; Zohary & Fahn, 1941; Stopp, 1958; Van der Pijl, 1972). Die belang van die higrochastiese openingsmeganisme van die kapsules van die Mesembryanthemaceae moet gesien word in die lig van die klimatologiese toestande waaronder hierdie plante groei. Gedurende die droë somermaande bly die sade in die vrugte ingesluit en word sodoende teen meganiese beskadiging beskerm. Eers wanneer die reënseisoen in die herfs aanbreek, kan die sade deur reëndruppels uit die vrugte vrygestel word. Die primitiewe tipe kapsule sonder hokvlerke of saadsakkies, kan moontlik in een reënbui leeggemaak word, maar die meer gevorderde tipes vrugte word meer geleidelik en in opeenvolgende reënbuie leeggemaak. Die kans van oorlewing is derhalwe beter in die gevorderde groepe, aangesien minder sade op 'n keer vrygestel word en al die saailinge nie tot niet sal gaan as ongunstige toestande die reënbui opvolg nie.

Opsomming

Die afstand sowel as die tempo van saadverspreiding is by ses verskillende spesies ondersoek. Hierdie spesies het 'n reeks gevorm van soorte met 'n primitiewe tipe kapsule, waar geen hokvlerke of plasentale knoppe voorkom nie, deur 'n soort waar slegs hokvlerke voorkom na soorte met 'n gevorderde tipe kapsule, waar beide hokvlerke en plasentale knoppe voorkom. Die gemiddelde afstand van saadverspreiding neem van die primitiewe na die gevorderde soorte

kapsules toe, terwyl die tempo van saadvrystelling afneem. Ruimtelike saadverspreiding word bevorder deur die teenwoordigheid van hokvlerke sowel as plasentale knoppe, terwyl die tempo van saadvrystelling deur die teenwoordigheid van hokvlerke vertraag word.

Die morfologiese uitbeelding van die sade beïnvloed ook die saadverspreidingsvermoë van 'n spesie. By die soorte waar die grootste persentasie van die sade baie naby aan die kapsule te lande kom is die sade meer hoekig en die oppervlak is baie onreëlmatig. By die soorte waar die sade gemiddeld verder vanaf die kapsule te lande kom, is die vorm van die sade baie meer vaartbelyn en die oppervlak is relatief glad.

By sommige spesies, byvoorbeeld *Micropterum papulosum*, word saadsakkies aangetref waarin 'n aantal sade ingesluit bly. Hierdie sade word nie maklik deur vallende waterdruppels vrygestel nie.

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CHROMOSOME NUMBER IN *THAMINOPHYLLUM* (ASTERACEAE-ANTHEMIDEAE)

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ABSTRACT

A chromosome number of $2n = 20$ has been found in all three species of *Thaminophyllum* (Asteraceae-Anthemideae) a small genus endemic in the Caledon district of the southwestern Cape. This number links *Thaminophyllum* more closely to *Inezia* ($n = 10$) than to other southern African Anthemideae for which chromosome numbers are known such as *Eriocephalus* which has $n = 9$. This number is also unusual in Anthemideae for which $n = 9$ and multiples are frequent.

UITTREKSEL

CHROMOSOOMGETAL IN *THAMINOPHYLLUM* (ASTERACEAE-ANTHEMIDEAE)

Chromosoomgetal van $2n = 20$ is gevind vir al soorte in die geslag *Thaminophyllum* (Asteraceae-Anthemideae) wat endemies in die Kaledon-distrik van die suidwes-Kaap voorkom. Hierdie getal verbind *Thaminophyllum* baie nouer met *Inezia* ($n = 10$) as met enige ander Suider-Afrikaanse Anthemideae waarvoor chromosoomgetalle bekend is; bv. *Eriocephalus* het $n = 9$. Hierdie getal is ook ongewoon in Anthemideae waar $n = 9$ en meervoude daarvan volop is.

INTRODUCTION

In collaboration with Pauline Bond, who has recently completed a revision of *Thaminophyllum* (Asteraceae-Anthemideae) (Bond, 1980), I undertook a chromosome study of the genus, until now cytologically unknown. *Thaminophyllum* is a genus of small shrubs comprising only three species, and is restricted to the mountains of the Caledon district of the southwestern Cape. It is allied to a distinctive group of southern African Anthemideae amongst which are *Lidbeckia, Inezia*, and, perhaps more distantly allied, *Adenanthellum, Eumorphia, Phymaspermum, Lasiospermum*, and *Eriocephalus*.

MATERIAL AND METHODS

Plants studied were wild collected cuttings (Table 1), rooted under mist spray conditions. Only mitotic chromosome counts were made. Root tips, collected at midday were placed in saturated aqueous p-dichlorobenzene solution for 6 hours, at refrigerator temperatures, then fixed in Carnoy's 3:1 ethanol-acetic acid. After a 6 minute hydrolysis in 10% HCl at 60 °C, root tips were squashed in lacto-propionic orcein (Dyer, 1963).

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TABLE 1.

Chromosome numbers in *Thaminophyllum*. All localities are in the Cape Province, South Africa, and voucher specimens are housed at the Compton Herbarium, Kirstenbosch Botanic Gardens, Cape Town (NBG)

Species	Haploid Number	Collection Data
T. latifolium	10	Caledon district, Voëlklip, Hermanus, above 8th Avenue, *Bond 1697.*
T. mundii	10	Caledon district, lower area of Highlands Forest Reserve, *Goldblatt 4771.*
T. multiflorum	10	Caledon district, Houw Hoek, *Goldblatt 4982.*

RESULTS AND DISCUSSION

Plants studied all had a similar karyotype with fairly large, acrocentric chromosomes, and a diploid number of $2n = 20$. This number is unusual in the Anthemideae, most genera of which have $n = 9$ (Heywood & Humphries, 1978) or multiples on this base. Amongst the African genera with which *Thaminophyllum* is allied, *Eriocephalus* has $x = 9$ (Nordenstam, 1967, 1969), *Lasiospermum* both $n = 10$ and 9 (Nordenstam, 1967), *Inezia* $n = 10$ (Turner & Lewis, 1965) and *Adenanthellum* (= *Adenanthemum:* Nordenstam, 1979) $2n = 30$ (Nordenstam, pers. comm.). Counts are unfortunately lacking for most relatives including *Eumorphia, Phymaspermum, Lidbeckia, Osmitopsis*, and *Peyrousia*.

On the basis of rather meagre chromosomal data, the number in *Thaminophyllum*, $n = 10$, supports Phillips' (1932) suggestion that the genus is probably more closely allied to *Inezia* (and to the uncounted *Lidbeckia*) than to *Eriocephalus*. The number of $n = 15$ *Adenanthellum* ($2n = 30$) is problematic, but this number may be triploid based on $x = 10$, which would link this genus to the $n = 10$ group of Anthemideae including *Thaminophyllum* and *Inezia*. *Lasiospermum*, in which both $n = 10$ and 9 are recorded, may possibly be related, but morphology suggests that this genus is closer to *Eriocephalus* than to other genera of southern African Anthemideae. Clearly many more counts are needed before full use can be made of cytological data in evaluating generic relationships and evolution within the group.

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SOME OBSERVATIONS ON THE ANATOMY OF *ARTEMISIA AFRA* JACQ.

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Abstract

The anatomy of *Artemisia afra* was investigated at the light microscope level, using fresh, paraffin and Spurr's-embedded stem, petiole, rachis, petiolule and leaflet material. The young stem consists of a uniseriate epidermis, a cortex of collenchyma and parenchyma, a poorly defined multilayered starch sheath and a ring of collateral vascular bundles surrounding an entirely parenchymatous pith. The primary phloem contains thick-walled sieve tubes. Oil ducts are spatially associated with the vascular bundles and starch sheath.

Artemisia afra has pinnatisect leaves. The main vein is surrounded by a poorly defined multilayered parenchymatous sheath. As in the stem, the phloem of the main vein contains thick-walled sieve tubes. A pair of adaxially situated oil ducts occur within the bundle sheath of the main vein. The anatomy of the rachis is similar to that of the petiole. The midrib of the petiolule contains a single adaxial oil duct, which is located within the bundle sheath. Similarily, the main vein of the leaflet is associated with a single adaxial oil duct. No oil ducts are associated with the second and third order veins of mature leaflets. The minor veins of the leaflets contain phloem transfer cells.

Uittreksel

WAARNEMINGS OOR DIE ANATOMIE VAN *ARTEMISIA AFRA* JACQ.

Die anatomie van *Artemisia afra* is ondersoek op die ligmikroskoop vlak. Dwarsdeursneë van die stingel, petiool, ragis, petioluul en pinna in was en plastiek ingebed sowel as vars materiaal is gebruik. Radiale lengtesneë is ook van die stingel gemaak. Die jong stingel word begrens deur 'n epidermis waaronder 'n buitenste kortekslaag van kollenchiem en 'n binneste kortekslaag van parenchiem voorkom. Die kollaterale vaatbondels word na buite begrens deur 'n swak gedefinieerde meerlagige setmeelskede. Die murg is geheel-en-al parenchimaties. Die floeëm van hierdie spesie bevat dikwandige sifvate. Oliekanale met omringende sekreetselle is met die vaatbondels en setmeelskede geassosieer.

Artemisia afra het gepinnatisekteerde blare. Die hoofaar van die goed ontwikkelde petiool word deur 'n swak ontwikkelde meerlagige parenchimatiese bondelskede omgewe. Soos in die stingel bevat die floëem van die hoofaar ook dikwandige sifvate. Twee adaksiale oliekanale is geassosieer met die bondelskede van die hoofaar voor. Die anatomie van die ragis stem ooreen met dié van die petiool. Die hoofaar van die petioluul bevat 'n enkele adaksiaal geleë oliekanaal, ingesluit deur die bondelskede. Netso bevat die hoofaar van die pinna ook 'n enkele adaksiaal geleë oliekanaal binne in die bondelskede. Geen oliekanale kom voor of is geassosieer met die tweede en derde orde are van volwasse pinnas nie. Floeëm oordragselle is waargeneem in die kleiner aartjies van die pinnas.

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Introduction

Artemisia afra Jacq., (Tribe : Anthemideae) commonly known as wormwood or wilde-als, is a member of the Compositae. *Artemisia* ranges from Ethiopia, through Eastern Tropical Africa, down into Southern Africa. *Artemisia* is widely distributed in the eastern part of South Africa, extending as far south as Stellenbosch (Hilliard, 1977).

Artemisia species have long been recognised as sources of essential oils (Brouk, 1975; Guenther, 1952; Sievers, 1947; Schery, 1972). *Artemisia afra* is one of the plants currently being studied as a source of essential oils in the Faculty of Agriculture at Fort Hare University.

The primary aim of this study was to examine the anatomy of the aerial parts of *Artemisia afra*, with a view to locating the oil ducts and their associated secretory cells. During this study, material containing only primary vascular tissues was used in determining the location of the oil ducts.

Material and Methods

All plant material used in this study was harvested in the field and immediately transferred to our laboratories for further processing. Suitable young and mature stem segments, petiole, rachis, petiolule and entire leaflets were fixed in either FAA (Sass, 1958) or in 4 % glutaraldehyde in 0,05M phosphate buffer, pH 7,0. Material fixed in FAA was dehydrated in a TBA series, and embedded in paraplast wax and sectioned at 10 μm on a Leitz rotary microtome. Glutaraldehyde-fixed material was dehydrated in an alcohol series and embedded in Spurr's resin. Serial sections were cut at 0,5 to 2,0 μm, with glass knives on an LKB Ultrome II. Wax embedded serial sections were stained in safranin fast green-gentian violet (Johansen, 1940) and mounted under coverslips in DPX synthetic mounting medium. Plastic sections were viewed either unstained, or stained in 0,05 % toluidine blue 0, pH 7,0 for 5 min on a hotplate (O'Brien, Feder and McCully, 1964) or in 0,05 % fluorecin-K in distilled water, for 20–30 min. All plastic sections were mounted in Entellan rapid mounting medium (Merk).

For localisation of oil ducts and confirmation of the presence of oils within the ducts, fresh material was sectioned on a Leitz freezing microtome at 15–20 μm and stained in Sudan IV (0,5 % w/v in 95 % ethyl alcohol) according to the procedure outlined in Johansen (1940). Selected sections were photographed with a Zeiss photomicroscope III, using brightfield, phase-contrast, and transmitted fluorescence optics.

Results and Discussion

1. *Stem*

The ribbed stem of *Artemisia afra* is bounded by a single-layered epidermis. The outer cortex consists of lamellar collenchyma (Fig. 1) which is especially well

developed beneath the ribs. The inner cortex consists of mixed parenchyma-chlorenchyma tissue and a poorly defined starch sheath, 1–2 cells in width (SS, Figs 1–2). The primary vascular bundles are collateral and are closely spaced. In Figures 1–2, the primary xylem and primary phloem are separated by a fascicular cambium, which apparently has not yet produced any secondary vascular tissues.

The phloem consists of sieve tubes and associated parenchymatous cells, including companion cells. Metcalfe and Chalk (1950) have reported that the phloem of Compositae sometimes contain lignified elements. During the present investigation, thick-walled sieve tubes were observed in stem and leaf material. These thick-walled sieve tubes are very conspicuous in transections stained with fluorecin-K, and viewed with fluorescence optics (Fig. 1). Judged by the relative fluorescence intensities, the sieve tubes are not lignified, but have thick cellulosic cell walls (compare rather weak fluorescence of walls of lignified xylem elements with strong fluorescence of walls of collenchyma and sieve tubes in Fig. 1). Further, when stained in toluidine blue O, the walls of the sieve elements typically were blue to purple in colour and not green as would be the case if they were lignified.

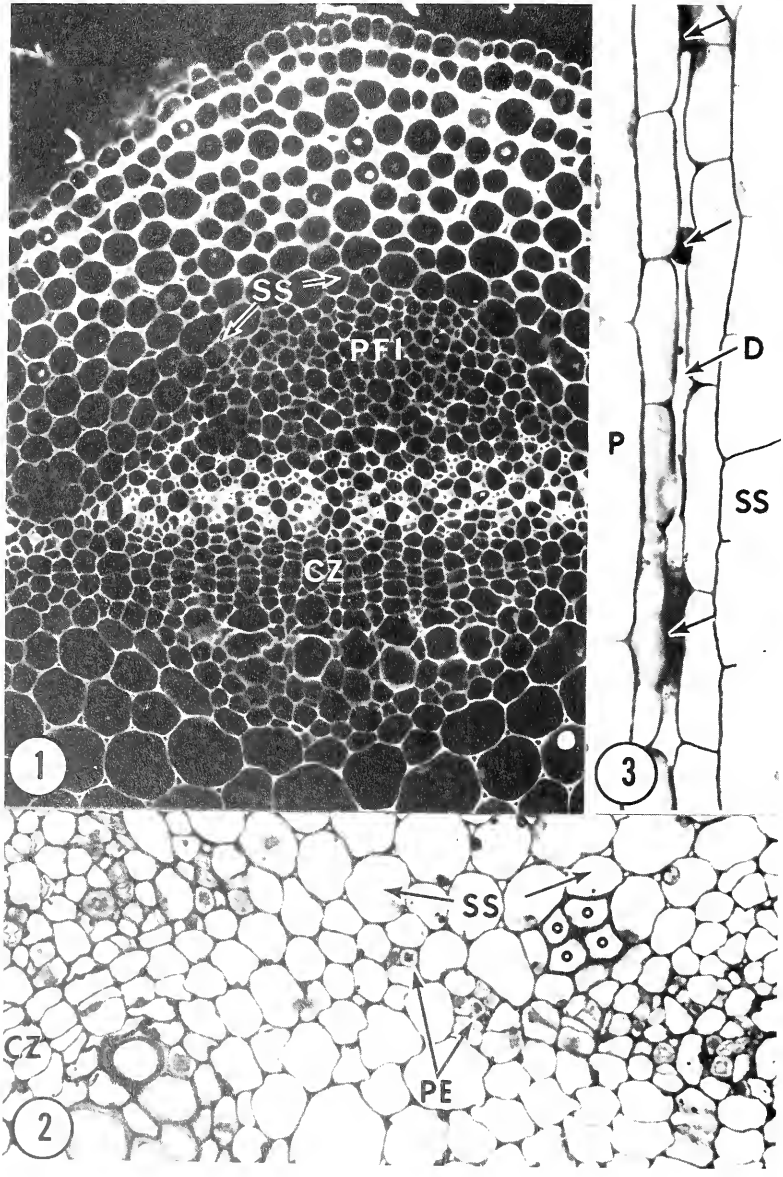
As mentioned, the vascular bundles illustrated in Figures 1–2 apparently are composed entirely of primary tissues. No secondary vascular tissues are evident. In such material the interfascicular regions are parenchymatous, with the exception of isolated patches of phloem elements, including thick-walled sieve tubes (PE, Fig. 2). Figure 2 shows an oil duct surrounded by four secretory cells (open circles) just beneath the starch sheath. Note that the walls of the secretory cells are more darkly stained than those of the surrounding parenchymatous cells. The oil duct is occluded with a densely stained substance. When viewed in tangential section (Fig. 3) the relationship of the relatively narrow oil duct to its surrounding secretory cells is clear. Three amorphous deposits are visible in this duct (unlabelled arrows). Similar sections stained in Sudan IV indicated that these deposits could be some form of oil.

Oil ducts and their associated secretory structures may arise within the plant either by lysigeny or schizogeny, or by a combination of both processes (Esau, 1965). Examination of transverse, tangential and radial longitudinal sections revealed that the ducts in the *Artemisia* stem are schizogenous in origin, that is, that they arise by schizogenous separation of the inner walls of the secretory cells.

2. *Petiole, Rachis, Petiolule and Leaflet*

.1 Leaf Architecture

In order to gain a more thorough understanding of the architecture of the compound leaf, whole leaves were cleared (Foster, 1952) and examined under the microscope. Venation of the individual leaflets is simple and, according to the classification system of Hickey (1973), brochidodromous. Each leaflet contains a single primary vein, from which a number of secondaries emerge.


SS
PFI
CZ
1
D
P
SS
3
SS
CZ
PE
2

The third order veins are weakly developed and few in number. Anatomical investigation indicated that the second and third order veins constitute the minor veins in leaflets of the *Artemisia* leaf. Areolation shape was found to be variable, but mostly quadrangular.

.2 Anatomy

.2.1 Petiole

As viewed in transection, the petiole consists of a single large crescentric collateral vascular bundle surrounded by parenchymatous ground tissue. The vascular bundle is delimited by a poorly defined parenchymatous sheath. As in the stem, the phloem contains thick-walled sieve tubes. Each midrib vascular bundle examined was associated with two adaxially situated oil ducts which were spatially associated with the bundle sheath (Fig. 4). As with the stem bundles, the midrib vascular bundle is surrounded by a multilayered sheath (Fig. 4).

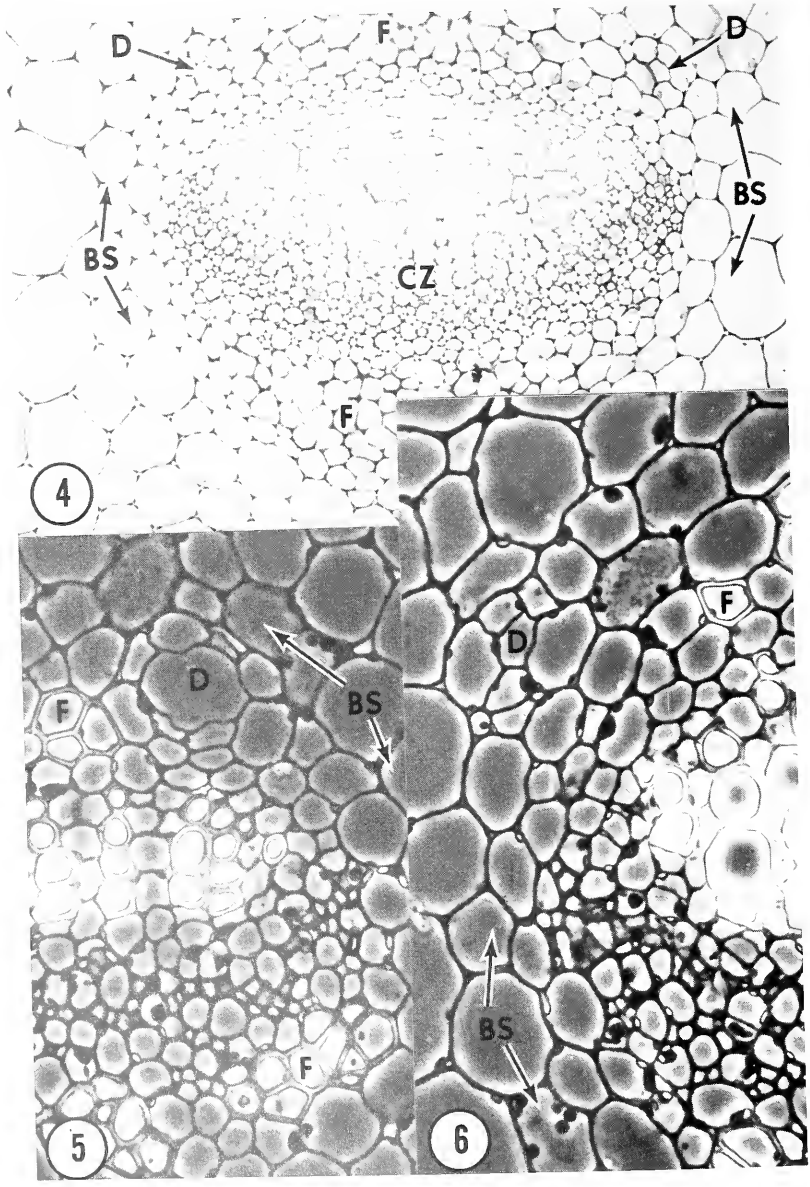
.2.2 Rachis

The anatomy of the rachis, as one might expect, was similar to that of the petiole (Fig. 4). Figure 6 shows one of two oil ducts situated beneath the bundle sheath of the main vein of the rachis. Fibres occur above and below this vascular bundle. Figure 5 shows part of a lateral vein of a rachis-petiole region. This vein has a single oil duct located above the protoxylem but beneath the bundle sheath. This vein constitutes the main vascular supply of the leaflet. As in the rachis (Fig. 6), fibres occur above and below the vascular bundles.

FIG. 1.
Fluorescence photomicrograph of a transection of part of a young stem. Note relatively weak fluorescence of walls of parenchymatous cells, including those of the cambial zone (CZ) and immature primary phloem fibres (PFI). Starch sheath (SS) delimits vascular from ground tissue. x 300.

FIG. 2.
Transection of a young stem, showing part of two adjacent primary vascular bundles. Some metaxylem elements are mature. Thick-walled cells immediately above the cambial zone (CZ) are sieve tubes. A poorly defined starch sheath (SS), delimits vascular from ground tissue. An oil duct, surrounded by four secretory cells (open circles) is associated with the bundle on the right. Phloem elements (PE) between bundles have thick walls, as do the metaphloem elements within the bundles. x 720.

FIG. 3.
Tangential section, showing part of an oil duct (D) similar to that shown in transection in Figure 2. The oil duct contains darkly stained material, presumably oil. The secretory cells are bordered by parenchymatous cells (P) to the left, and starch-sheath cells (SS) to the right. x 720.


D
F
D
BS
BS
CZ
F
4
D
F
BS
F
5
F
D
BS
6

.2.3 Petiolule and Leaflet

The petiolule of each leaflet of *Artemisia* is winged and contains a large, acentrically situated main vein, together with associated minor veins. Figures 7–8 are transections of the same main vein at two levels of the leaflet. Of interest is the fact that the bundle sheath contains fairly conspicuous chloroplasts. Figure 7 shows the arrangement of the vascular tissues and the single adaxial oil duct near the base of the leaflet; Figure 8 near the tip of the leaflet. Oil ducts were not found in veins smaller than the one shown in Figure 8.

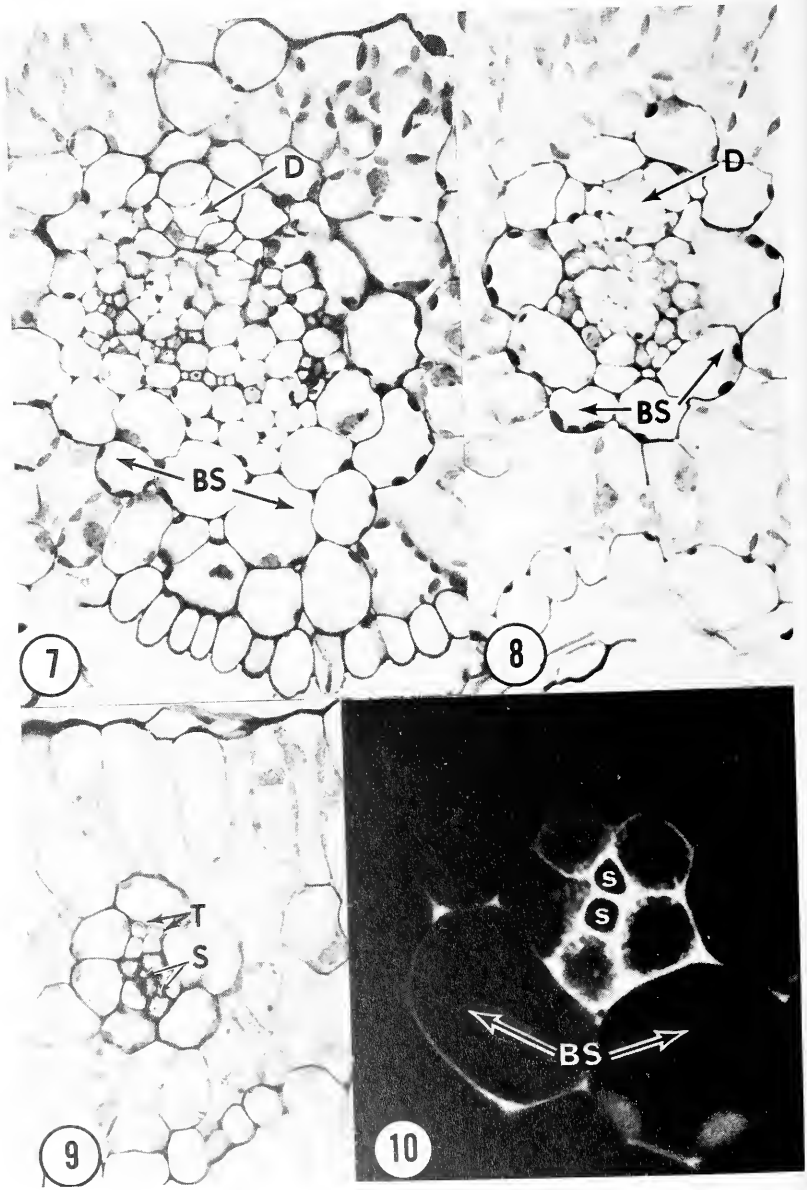
During the investigation, it became apparent that the remaining two orders of veins (i.e. second and third orders) contained parenchymatous cells, with conspicuously thickened cells walls. These parenchymatous cells were associated with the sieve tubes. Figure 9 shows a third order vein with two sieve tubes and two tracheary elements. At this magnification, the wall thickenings of neighbouring parenchymatous cells are discernible. Moreover, fluorescence microscopy revealed that these cells are transfer cells. Figure 10 shows two sieve elements surrounded by 5 transfer cells with prominent wall ingrowths. Note that the wall ingrowths are more conspicuous on the cell walls adjacent to the sieve tubes than elsewhere.

Transfer cells are not uncommon in the Compositae. Gunning, Pate and Green (1970) list 13 genera in which transfer cells have been positively identified. The transfer cells of minor veins have been implicated in the retrieval and transfer of solutes to the sieve tubes, from both the transpiration stream and the pathways of photosynthates (Pate and Gunning, 1972). Gunning and Pate (1974) and Gunning, Pate and Briarty (1968) have suggested that the initiation of wall ingrowths in minor veins coincides with, or slightly precedes commencement of export of photosynthates from the leaf. Further development of wall ingrowths parallels build-up in export activity.

FIG. 4.
Transverse section of petiole, showing crescentric collateral vascular bundle. Bundle sheath (BS) is poorly differentiated and lacks chloroplasts. The xylem and phloem apparently are entirely primary, although separated by a cambial zone (CZ). Two adaxially located oil ducts (D) can be seen inside the bundle sheath. The vascular bundle is capped by fibres (F) above and below. x 290.

FIG. 5.
Phase contrast photomicrograph of a lateral vein in the rachis—petiolule region. This vascular bundle contains a single adaxial oil duct (D), surrounded by several secretory cells. Fibres (F) occur above and below the vascular bundle. The vascular bundle, including the oil duct and its associated secretory cells, is ensheathed by a parenchymatous bundle sheath (BS). x 720.

FIG. 6.
Phase contrast photomicrograph showing part of the main vein of the rachis. One of two adaxial oil ducts (D) is visible. As in Figure 5, the vascular tissue is bordered by fibres (F) and surrounded by an achlorophyllous parenchymatous bundle sheath (BS). x 720.


D
BS
7
D
BS
8
T
S
9
S
S
BS
10

Conclusion

During the investigation oil ducts were localized in young stem and leaf material. These oil ducts were associated with the primary vascular bundles in the stem and with primary, or first order veins of the petiole, petiolule and leaflets, but not with the minor veins. It is possible that these oil ducts terminate with the primary vein system in the leaflets of *Artemisia*.

The phloem of this species requires further mention, due to the presence of thick-walled, apparently non-lignified sieve elements in stem and leaf material and the association of minor vein sieve elements with transfer cells. The nature of the sieve element cell wall and the structural relationship of sieve elements to transfer cells in minor veins are currently being investigated.

Acknowledgements

The South African Council for Scientific and Industrial Research is acknowledged for a running expenses grant to the senior author. The University of Fort Hare Research and Capital Equipment Committee is acknowledged for funds enabling the senior author to purchase capital equipment used in this study. We wish to express our grateful thanks to Professor Ray F. Evert, of the Botany Department, University of Wisconsin at Madison, for reviewing and commenting on this article. The authors are indebted to Professor E. H. Graven of Fort Hare University for making plant material available to us.

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Fig. 7.
Transection of main vein near base of leaflet. An oil duct is located immediately above the protoxylem. Bundle sheath (BS) contains chloroplasts. x 640.

Fig. 8.
Transection of main vein near tip of leaflet. As in Figure 7, the oil duct is located adaxial to the protoxylem. Bundle sheath (BS) contains chloroplasts. x 640.

Fig. 9.
Transection of minor vein of leaflet, with two sieve tubes (S) and two tracheary elements (T). Bundle sheath cells have chloroplasts. Thickenings of the phloem parenchyma cell walls are discernible at this magnification. x 640.

Fig. 10.
Fluorescence photomicrograph of minor vein of leaflet, showing two elements (S) surrounded by transfer cells with prominent wall ingrowths are most strongly developed adjacent to the sieve elements. Tracheary elements are not discernible in this micrograph, due to weak fluorescence of their walls. x 900.

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Jl S. Afr. Bot. 46 (2): 207–211 (1980)

A NEW SPECIES OF *EUPHORBIA* (SECTION *TETRACANTHAE*) FROM THE TRANSVAAL

L. C. Leach*

Abstract

A new succulent *Euphorbia, E. louwii* from the Tranvaal, is described.

Uittreksel

'N NUWE *EUPHORBIA* (SEKSIE *TETRACANTHAE*) SOORT VAN TRANSVAAL

'n Nuwe vetplant *Euphorbia, E. louwii* vanaf die Transvaal word beskryf.

Euphorbia louwii Leach, sp. nov. ad sectionem *Tetracanthas* Pax clare pertinens sed ab aliis omnibus epidermide veneta vel lazulina et a fere omnibus ramis multangularibus, podariis spina quinta et cyathiis bisexualibus secundariis ex axillis bractearum cyathiorum lateralium prodientibus manifeste differens; habitu erecto *E. complexae* R. A. Dyer et fortasse ei arctissime affinis, etiam ad *E. aeruginosam* Schweick. arcte cognata sed ab ambobus ramis venetis vel lazulinis 5–7 angularibus, stylis longioribus e basi libris facile distinguenda, ab illa radicibus minus rhizomatosis et ab hac habitu erecto, ramis longioribus pauciramosis angulatis vel sulcati-costatis vix subcylindricis, spinis brevissimis et floribus masculis brevioribus distinctissima.

Typus: Transvaal: *Leach, W. J. Louw & P. I. Rossouw 15555* (K, PRE, holo.; SRGH).

Frutex succulentus, spinosus, e basi ramosus, superne parcissime ramificans. *Rami* veneti vel lazulini, 5–7-angulati, angulis sinuato-tuberculatis crenulatisve, inter angulos leviter concavi, pallide flexuoso-vittati, in sicco longitudinaliter costatis saepe fere alatis; erecto-ascendentes, c. 1 cm diam. usque ad c. 50 cm alti. *Folia* anguste ovato-acuta, c. 1,5 mm longa, cito caduca, cicatricibus inconspicuis. *Podaria* separata, plus minusve 1,5 mm lata, obtuse truncata, decurrentia, basi anguste subobtusa, usque ad 10 mm longa, castanea purpurascentia; *spinae* aciculares quinque; illis paris inferioris, 5–6 (10) mm longis, aliquanto divergentibus, late vel saepe horizontaliter patentibus, interdum leviter deflexis; illis paris superioris 1,5–3 mm longis, late divergentibus, aspectu laterali suberecto-patentibus, folii cicatricis in quoque latere dispositis; quinta usque ad 1 mm longa, solitaria, podario prope basin, horizontaliter patenti. *Inflorescentia* cymosa more sectionis praeter cyathia tertiaria e bracteis cyathiorum lateralium prodientia, non

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Accepted for publication 29th September, 1979.

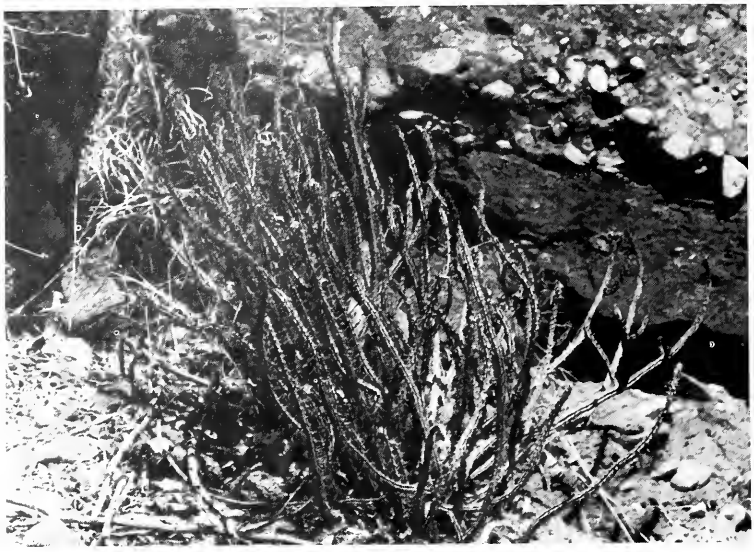

FIG. 1.
Euphorbia louwii: plant ± 500 mm high at the type locality near Marken; *Leach et al. 15555.*

axialiter disposita. *Pedunculus* bibracteatus, c. 1,5 mm longus; bracteae basi carnosae, semicirculares, c. 1 mm longae lataeque; *rami cymarum* c. 1 mm longi, bracteis oblongo-obovatis, denticulatis, c. 1,5 mm longis, 1 mm latis instructi. *Involucrum* obconice cyathiforme, c. 3 mm longum, 3,5–4 mm diam. glandulis inclusis; *glandulae* 5, transverse ellipticae, leviter irregulariter foveolatae, flavae, 1,5–2 mm × 0,75 mm; *lobi* 5, plus minusve obovati, profunde fimbriato-dentati, c. 1,5 mm longi latique. *Flores masculi* plerumque 10, bracteolis filiformibus aliquot in fasciculis distinctis 5, dispositi; fasciculi unusquisque floribus 2, bractea lata, laciniata, fimbriata interne subtentus; *pedicelli* ad 3 mm longi; *filamenta* c. 0,75 mm longa. *Flos femineus* subsessilis, ovario obtuse trigono, pedicello c. 0,75 mm longo, in perianthio rudimentali insidenti; *ovulum* obturamento, cucullato, aliquanto longo, leviter bilobato suspensum; *styli* graciliores, e basi libri, patulo-recurvi, interdum levissime ventraliter sulcati et ad apicem leviter emarginati, 2,75–3,25 mm longi. *Capsula* obtuse 3-lobata, c. 3 mm diam., 2,75 mm alta, initio viridis demum purpureo-ardesiaca; *semina* immatura, plus minusve anguste ovoidea, ruguloso-verrucosa.

A spiny, succulent *shrub*, branching freely from the base but very sparingly above; *branches* 5–7-angled, slightly concave between the lightly sinuate-tuberculate or crenulate angles, in dry periods becoming deeply sulcate and

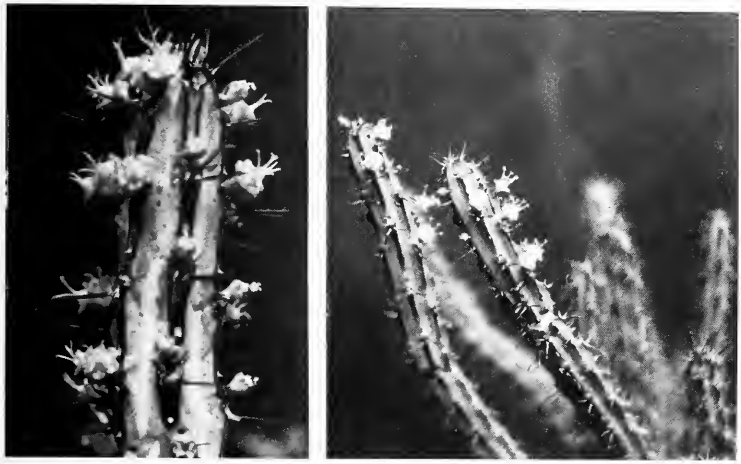

FIG. 2.
Cuttings of *E. louwii* flowering in cultivation at SRGH. Left: showing long styles and right: far exserted ♂ flowers.

longitudinally ribbed or almost winged, with the spine shields withdrawn slightly below the level of the surface of the ribbed angle, about 10 mm diam., ascending-erect, up to ± 500 mm high (exceptionally up to 1 m in shade, then becoming subcylindric, longitudinally sulcate rather than angular and somewhat trailing unless supported), grey-blue or greenish-blue with a paler, slightly flexuose, longitudinal blue stripe between the angles, often heavily purple mottled and sometimes becoming yellowish when exposed to full sun. *Leaves* narrowly ovate-acute, ± 1,5 mm long, quickly caducous, leaving a very inconspicuous transverse scar. *Spine shields* separate, ± 1,5 mm wide at the obtusely truncate apex, up to 10 mm long, decurrently tapering to the small subobtuse base, chestnut to purplish in colour, bearing 5 slender, needle-like *spines*, the lower of the two pairs 5–6 (10) mm long, divergent but not very widely so, widely to horizontally spreading or slightly deflexed, 10–15 mm apart along the angles, the upper pair 1,5–3 mm long, widely divergent on each side of the leaf-scar, erectly spreading to erect when seen from the side, and the fifth up to ± 1 mm long, solitary, distant, horizontally spreading from near the base of the spine shield. *Inflorescence* of the pattern usual for the section with a horizontally arranged cyme of three cyathia; however, additional cyathia, when developed, arise in the axils of the bracts supporting the lateral cyathia, not axially arranged in relation to the peduncle. *Peduncle* bibracteate, ± 1,5 mm long; *bracts* fleshy at the base, more or less semicircular, ± 1 mm × 1 mm, each subtending a bibracteate *cyme branch* ± 1 mm long; *bracts* oblong-obovate, fringe-toothed, ± 1,5 mm long, 1 mm

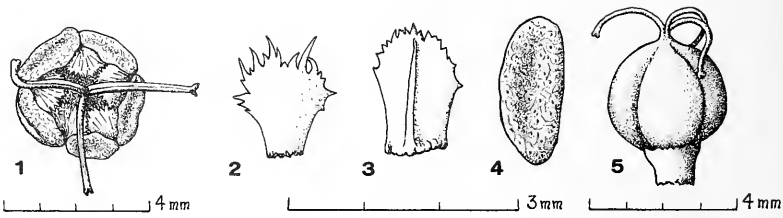

FIG. 3.
Euphorbia louwii: (1) Cyathium, showing long styles (2) Involucral lobe (3) Bract (4) Gland; all from *Leach et al. 15555* (5) Capsule from *Louw* sub *Leach 14872.*

wide. *Involucre* obconic-cup-shaped, initially merging with the cyme branch without any perceptible articulation (the whole quite funnel-shaped), ± 3 mm long, 3,5–4 mm diam. including the glands; *glands* 5, transversely elliptic, shallowly irregularly pitted, yellow, 1,5–2 mm × ± 0,75 mm; *lobes* 5, more or less obovate, deeply irregularly fimbriate, ± 1,5 mm × 1,5 mm. *Male flowers* 10, with a few filiform bracteoles, arranged in 5 distinctly separate fascicles, each subtended and closely enwrapped by a lobe on the outside and a deeply laciniate fimbriate, 2 mm long, broad bract on the inside, which forms a pocket at its base for about 1/3rd of its length, into which the 2 male flowers are inserted; *pedicels* up to 3 mm long; *filaments* ± 0,75 mm long. *Female flower* subsessile; ovary obtusely trigonous, seated on a rudimentary, crenulate, pedicel-perianth ± 0,75 mm long; *ovule* suspended beneath a rather long, slightly 2-lobed, hood-like obturator; *styles* very slender, free to the base, spreading recurved, sometimes very slightly ventrally sulcate and slightly emarginate at the enlarged apex, 2,75–3,25 mm long. *Capsule* obtusely 3-lobed, ± 3 mm diam., 2,75 mm high, initially green becoming dark slate-purple when mature, seated on a pedicel-perianth ± 0,75 mm long, almost 2 mm diam.; *seeds* immature, more or less narrowly ovoid, rugulose-verrucose.

It is with great pleasure that this distinctive new species is named for my friend Dr W. J. Louw who has, for very many years, been associated with the study of succulent plants, especially of *Euphorbia*, as may be seen from the pages of White, Dyer & Sloane, *The Succulent Euphorbieae* (1941).

E. louwii has a very restricted distribution in the north-western Transvaal, an area in which several other endemic species of the genus such as *E. clivicola* R. A. Dyer and *E. waterbergensis* R. A. Dyer are known to occupy similarly restricted areas.

Clearly belonging in section *Tetracanthae* this shrubby new species differs from all others of that section known to me, in the bluish colour of its epidermis, and from most, in its 5–7-angled branches and the fifth spine which is regularly developed near the base of the spine-shield (similar "extra" spines occur quite

frequently but irregularly in *E. aeruginosa* and occasionally in *E. ambroseae* Leach, which are also members of the same section). An important difference in the arrangement of the inflorescence of *E. louwii* is to be observed in the development of secondary bisexual cyathia from the axils of the bracts supporting the original lateral cyathia, after the manner of *E. knuthii* Pax, *E. griseola* Pax and other species of that group in which the ovary is far exserted from the involucre. In *Tetracanthae* secondary bisexual cyathia are normally developed only axially, above and below the initial central cyathium. This new member of the section appears possibly to be most closely related to *E. complexa*. This latter is of very limited distribution in the eastern Transvaal lowveld at about 300 m altitude in an area of relatively high rainfall, and develops a massively rhizomatous root system from which clonal groups usually develop, so differing considerably in both habit and habitat, as well as morphologically, from its north-western relative. There is also a close relationship with *E. aeruginosa* from the Limpopo valley but in addition to its colour and multi-angled branches *E. louwii* is further distinguished by its very much shorter spines, styles free to the base and shorter male flowers.

All the species with which comparisons are made have retained their respective characteristics over many years in cultivation in the author's garden.

Material Examined

TRANSVAAL—2328 (Baltimore): ± 14 km E. of Marken (-CB), sandstone and conglomerate hillside, ± 925 m alt., 1.xi.1975, *Leach, W. J. Louw & P. I. Rossouw 15555* (K, PRE, SRGH), idem cult. SRGH, fl. 1978 (K, PRE, SRGH); ibid., tall subscandent plant in shade, with old parts subcylindric, woody and unarmed, *15555A* (PRE, SRGH), ibid., juvenile plant, *15555B* (PRE); ibid., *W. J. Louw s.n.*, cult. PRE, 29.viii.1969, sub *7434* (PRE), cult. SRGH, fl. & fr., 12.x.1973, sub *Leach 14872* (K, PRE, SRGH).

——2428 (Nylstroom): near Strikfontein Store (-AB), on flat black stones, v.1948, *W. F. Bayer s.n.* (PRE).

Acknowledgements

I wish to express my thanks to:

The Director, Botanical Research Institute, Pretoria, for the facilities of the herbarium, and to Dr W. J. Louw and the late Mr P. I. Rossouw for their assistance in the field when the type material of *E. louwii* was collected.

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DISA CARDINALIS LINDER (ORCHIDACEAE), A NEW SPECIES FROM THE CAPE PROVINCE

H. P. Linder

(Bolus Herbarium, University of Cape Town)

Abstract

Disa cardinalis Linder, sp. nov. (Orchidaceae), is described from the Riversdale area of the Cape Province.

Uittreksel

DISA CARDINALIS LINDER (ORCHIDACEAE), 'N NUWE SOORT VANAF KAAPLAND

Disa cardinalis Linder, sp. nov. (Orchidaceae), van die Riversdale gebied van Kaapland word beskryf.

Introduction

A red-flowered *Disa*, previously regarded as a colour form of *Disa tripetaloides* (L.f.) N.E.Br., is in cultivation, and is being used in a hybridization programme. Taxonomic studies on the *Disinae* showed that this taxon should be recognized as a distinct species. In view of the bright red colour of the flowers the name *Disa cardinalis* is proposed.

Taxonomy

Disa cardinalis Linder, sp. nov., differt a *D. tripetaloides* (L.f.) N.E.Br. floribus majoribus et carminis.

Plants slender, erect, 300–600 mm tall; tubers testicular, c. 15 mm long; roots thick, unbranched, villous; slender white stolons with bracts regularly produced. *Leaves* at the base of the stem semi-erect, very narrowly elliptic, acute, 50–100 mm long, clustered, 6–10; the rest distant on the stem, 15–30 mm long, very acute to acuminate, completely sheathing. *Inflorescence* sub-imbricate, up to 150 mm long and with 8–20 flowers; bracts narrowly ovate, subacuminate, 10–25 mm long, as long as or slightly longer than the ovaries; flowers c. 25 mm in diameter, bright red. *Dorsal sepal* erect, galea 10–15 mm tall 8–10 mm wide and 6–8 mm deep, more or less acute, narrowly ovate in front view; spur conical, obtuse, c. 4 mm long. *Lateral sepals* patent, the apex often recurved, elliptic, obtuse to rounded, 18–28 mm long, apiculus 1 mm long. *Petals* included in the galea, horizontal, flanking the anther, narrowly oblong-trapezoid, fused to the rostellum,

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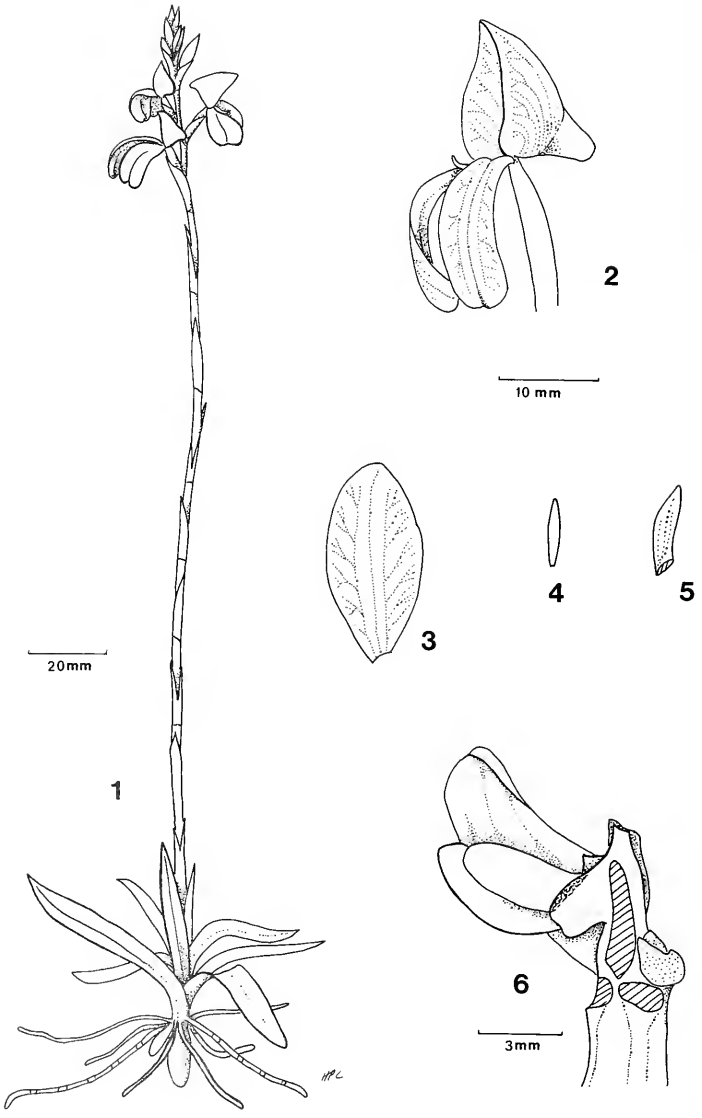

FIG. 1.
Disa cardinalis, from *Linder 1716* (Type). 1. Whole plant, 2. flower, 3. lateral sepal, 4. lip, 5. petal, 6. rostellum, anther and stigma.

the apex curved over the anther, 6–7 mm long and 2 mm wide. *Lip* patent, narrowly rhomboid, 6–7 mm long and 1–2 mm wide, subacute. *Rostellum* tri-lobed, lateral lobes erect, 3–4 mm tall, shallowly canaliculate, central lobe a small fold between the lateral lobes; anther horizontal, 3 mm long, viscidia globular, caudicles 2 mm long; stigma equally tri-pulvinate, sessile at the base of the rostellum, angled at 45°, c. 1,5 mm in diameter.

Type: Riversdale, Garcias Pass, along streams, alt. 600 m, 15.xii.1977, *Linder 1716* (BOL, holotype; K, PRE).

This new species is part of the *D. tripetaloides* group, which is allied to *Disa uniflora* Berg. It can readily be recognized from its close relatives by the bright red flowers (*D. tripetaloides* is white, pink or yellow) which are about a third larger than in *D. tripetaloides*. The lateral sepals are 18–28 mm long, as opposed to 10–15 mm for *D. tripetaloides*.

Eco-geographically it is also separated from *D. tripetaloides*. The latter taxon is distributed along the Cape fold mountains from Stellenbosch to Port Shepstone. Along the Langeberg it occurs on the wet south-facing slopes of the range. *D. cardinalis* is restricted to the dry northern slopes of the range, between Barrydale and the gorge of the Gouritz River. Here it grows on stream-banks, often among rocks. The stoloniferous growth probably offers some protection to the plants against being washed away during floods, and also results in the development of clusters of plants.

The climate in the habitats can only be guessed at, as the southern slopes of the range have a high (but as yet unquantified, probably more than 1000 mm p.a.) rainfall, and frequent wet fogs from south-easter winds, while the Karoo to the north of the range receives scarcely more than 250 mm p.a. (W.B. 29). The rainfall is fairly evenly distributed over the year. The vegetation of the area has been described by Muir (1929, p. 60).

Collections Studied

Barrydale, ex hort. Kirstenbosch, 1934, *s.l.* (BOL); Riversdale, Garcias Pass, October 1904, *Leipoldt* in Bolus *11381* (BOL, PRE); Riversdale, Garcias Pass, December 1977, *Linder 1716* (BOL, K, PRE).

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Book Reviews

Applied and Fundamental Aspects of Plant Cell, Tissue and Organ Culture, edited by J. Reinert and Y. P. S. Bajaj, with pp. xvi + 803 and 181 figures. Berlin, Heidelberg, New York: Springer-Verlag, 1977. DM 190, US $83.60.

This book, consisting of seven chapters written by a total of 49 contributors, covers a whole array of disciplines, techniques and applications in the general area of plant tissue culture. The treatise contains a contribution by Dr J. Button, a South African tissue culture researcher formerly of the University of Natal, Pietermaritzburg and Dr J. Kochba, an Israeli horticulturalist who spent 1972 on sabbatical leave in the Department of Botany at the University of Natal. Their contribution is on tissue culture in relation to the citrus industry and reflects the high standard of botanical research carried out at the University of Natal.

The book is well-suited to the shelves of those institutes where TC research is of a multi-disciplinary nature. Researchers with a more specialized interest would probably concern themselves with only a few chapters at most. Chapters are conveniently organized and both the subsections and the material within them follow a logical and progressive sequence: logical, in that early history, current status of research, scope and literature are well discussed; and progressive, in that areas of more or less ever-increasing complexity follow one upon the other.

It is probably inevitable that much of the material presented reflects the labours of the contributing authors themselves, but good editorship has resulted in a unitary presentation that is not unpleasant. There are few typographical errors (e.g. under Acknowledgments in the Button and Kochba chapter Fig. 1 should read Fig. 2).

One of the most interesting contrubutions is that of C. J. Jensen on monoploid production by chromosome elimination, in Chapter II under Haploids. This so-called bulbosum technique is now finding application in plant breeding programmes. Chapter IV, which deals with protoplasts, somatic hybridization and genetic engineering assesses the present status of knowledge and outlines the possible future approaches in applying methodology from the medical and bacteriological sciences to higher plant cell systems. Uses of recombinant DNA, plasmid transfer, transduction, transformation and mutagenesis are touched on, as are aspects of cellular organelle and organismal transfer.

This book is expensive, but it is a reference work and should prove good value for the investment.

Chris H. Bornman

Genetic and Molecular Basis of Plant Pathogenesis, by J. E. Vanderplank, with pp. xi × 167, 3 figures and 36 tables. Berlin, Heidelberg, New York, Springer-Verlag, 1978. Volume 6 in the series "Advanced Series in Agricultural Sciences". Cloth DM 48, US $24.00.

This volume is the third on Plant Pathology in the Advanced Series in Agricultural Sciences. Typographically the text is accurate and well indexed. The format is modern and the style is succinct. However, the frontispiece plate of precambrian fossils is somewhat incongruous and the figures of amino acid structures are inappropriately elementary in an advanced treatise. Schematic models to illustrate the essence of Dr Vanderplank's postulate would have been a worthwhile supplement to the text. There is a large compilation of useful data tabulated in an abridged form which makes this volume a recommended reference book for plant pathologists. However, there is a tendency towards an excessive and unnecessary use of footnotes to tables.

Dr Vanderplank, internationally recognised for his work on quantitative epidemiology, has set out to achieve two objectives in this volume: firstly, to provide further evidence for, and clarification of, his controversial views on the population genetics of pathogens and host plants and, secondly, to provide evidence for, and to derive a unifying hypothesis on the molecular basis of pathogenesis, host resistance and host specificity.

The author's familiarity with, and eminence in the epidemiological field are exemplified in chapters one, six and seven, which incidentally should have been arranged consecutively. The clear, purposeful and in-depth treatment of the population genetics and the genetic basis of resistance should clear-up much of the confusion and misinterpretation that arose from his earlier publications and which probably were the causes of much of the criticism levelled at his ideas. Chapters one, six and seven are for general readership by plant pathologists and may be read independently. These chapters are certainly a further contribution by Dr Vanderplank to rationalizing thought and practice in quantitative epidemiology.

The same cannot be said for the rest of the volume which is about Dr Vanderplank's protein-for-protein hypothesis. In the author's inimitable way he makes his opening gambit (lines 1–3, chap. 2): "In diseases in which host and pathogen are involved gene for gene, susceptibility involves the copolymerization of protein from the host with protein from the pathogen". This unsubstantiated statement at once suggests that this volume is not suitable for the uninitiated and inexperienced—further reading confirms this viewpoint. Dr Vanderplank will be judged to have ventured beyond the ambit of his direct experience. Evidence compiled from more than 300 references spanning 50 years or more, is admittedly well collated, convincingly arranged and demonstrates the author's originality and considerable perspective. However, neither the manner of presentation of speculative, circumstantial and tenuous evidence nor the hypothesis derived from it are well placed in a text such as this. For example, the data in table 3.6 (p. 61) show (statistically that is) no significant difference in resistance at 15C and 25C of Var. Appler in seedling and juvenile stages. Yet this is the type of unconvincing data the author uses to 'prove' the validity of his hypothesis which is largely based on the thermodynamics of protein copolymerization. The author relies heavily on the frequently observed loss of host resistance in gene-for-gene systems at elevated temperatures to prove his point. A perusal by the author of readily available data on energy budgets of potato and wheat plants with diverse leaf forms at different ambient temperatures and air movement surely would have introduced some caution into his extrapolations from ambient to internal leaf temperatures.

Brief reference, without any in-depth, objective evaluation, is made by Dr Vanderplank to the very vast and complex subjects of common antigens, non-protein biopolymers and host selective toxins (chapters 4, 5 and 8) essentially with a view to detracting from them as determinants of the fate of host-pathogen interrelationships.

The pre-eminence of this South African author in the field of epidemiology will certainly mean that this volume will have wide readership among plant pathologists in South Africa and abroad. I hope I am proved wrong but I believe that Dr Vanderplank's viewpoints on the molecular basis of plant pathogenesis will receive neither the local nor international acclaim that accompanied the publication of his epidemiological works.

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n-ALKANES IN *PTEROCELASTRUS* LEAF WAX

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Abstract

The n-alkanes in the leaves of three *Pterocelastrus* species are compared to each other. All specimens except one contain C_{29} as the primary alkane. One specimen of *P. rostratus* contains C_{28} as largest component. A negative correlation exists between total alkane content and the observed number of alkanes of different chain lengths. Intraspecific variation is larger than interspecific variation so that no taxonomic conclusions can be drawn from the observed patterns.

Uittreksel

n-ALKANE IN *PTEROCELASTRUS* BLAARWAS

Die n-alkane in die blare van drie *Pterocelastrus*-spesies word met mekaar vergelyk. Al die eksemplare behalwe een bevat C_{29} as die primêre alkaan. Een eksemplaar van *P. rostratus* bevat C_{28} as grootste komponent. 'n Negatiewe korrelasie bestaan tussen totale alkaaninhoud en die waargenome aantal alkane van verskillende kettinglengtes. Intraspesifieke variasie is groter as interspesifieke variasie sodat geen taksonomiese gevolgtrekkings uit die waargenome patrone gemaak kan word nie.

Introduction

The presence of n-alkanes as a constituent of leaf "external" (cuticular) and "internal" (cell content) waxes and their importance as a taxonomic criterion have been extensively discussed (Eglinton & Hamilton, 1967; Herbin & Robins, 1969) and applied to taxonomic problems by various authors.

Recent work has shown a possible relationship between species specific wax composition and insect susceptibility in *Trifolium* spp. (Thompson & Knight, 1978). This would seem to indicate that the wax composition, as well as the amount formed, is under genetic control and therefore could be used as a valid taxonomic attribute of a species. This is in agreement with Corrigan, Timoney & Donnelly (1978) who found that the alkane patterns of the leaves of *Galium* and *Asperula* do not change with plant age or geographical location and may be used as a taxonomic tool.

Herbin & Robins (1968) found an increase in carbon chain length with increasing age in several Gymnosperms, as was also found by Franich, Wells & Holland (1978) in *Pinus*. Similar results were obtained by Bianchi & Corbellini (1977) with leaves of *Triticum*. These authors therefore imply that the alkane composition of leaves cannot be used as a taxonomic attribute. This is also the

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conclusion to which Smith & Martin-Smith (1978) came after examination of the n-alkanes of *Saccharum* where they found that the intraspecific variation was larger than the interspecific variation.

No definite conclusions as to the suitability of this method for the examination of any taxon can thus be drawn.

During a study of *Pterocelastrus* Meisn. it was necessary to identify vegetative plant material of this genus unequivocally. Such material is more than ordinarily difficult to identify, due to the great similarity to members of other closely related genera. Proof of the difficulty of identification can be found in nearly any herbarium where non-fruiting material of especially *Maytenus oleoides* and *Pterocelastrus tricuspidatus* are mixed or misidentified. It was therefore deemed necessary to use chemotaxonomic characteristics to help with the identification.

G.L.C. determinations of the alkane composition of leaf waxes are relatively easy to perform and not unduly time-consuming. This approach was therefore chosen, especially with due regard to the equivocal results reported in the literature, so that recommendations as to the suitability of this method in *Pterocelastrus* and allied genera can be given.

Such an approach is necessary because the alkanes of any of the representatives of the Celastraceae have not been previously studied. No reference to this class of compounds can be found in the very complete treatment of the chemical compounds of the Celastraceae by Brüning & Wagner (1978).

Due to the known differences between "external" and "internal" leaf wax composition of higher plants (Herbin & Robins, 1969), and the possible differences between leaves of different ages, it was decided to analyse the total wax n-alkane component of leaves from an entire branch so that cuticular and internal alkanes of young and old leaves contribute to the pattern.

Suitable material of three species of *Pterocelastrus* could be obtained, and this was used in the analysis.

Material and Methods

Approximately 100 g (dry mass) of early summer leaves were obtained from each plant by removing all leaves from at least one branch of each of the specimens mentioned in Table 1. Voucher specimens of each sampled plant were deposited in the herbarium of the University of Potchefstroom.

The air-dried leaves of each plant were reduced to powder in a Retsch-mill and approximately 0,2 g samples of the thoroughly mixed leaf material were removed and accurately weighed. An internal standard of 0,02 $\mu\ell$ of n-heptadecane (C_{17}) in 10 $\mu\ell$ CCl_4 and a marker of 0,02 mg n-tetratetracontane (C_{44}) in 10$\mu\ell$ CCl_4 for determination of relative retention times, were added. C_{17} and C_{44} standards were chosen because none of the sampled specimens contained demonstrable amounts of these alkanes. After addition of 1 mℓ CCl_4 the mixture was shaken for 30 minutes at 45 °. All the following steps were done at this temperature to ensure

TABLE 1

All voucher numbers refer to specimens collected by D. J. Botha and J. Coetzee. Alkane concentrations are expressed as percentage of the total with trace quantities not indicated.

No.	Species	Voucher No.	Locality	Carbon Chain Length																						Total alkanes mg/g dry mass
				12	14	16	18	19	20	21	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	
1	*P. echinatus*	1603	Port Shepstone	0,2											3,3	4,2	77,3	1,8	10,7	0,7	1,1					0,34
2	*P. echinatus*	1886	Barnardsvlei		0,3	0,2									0,9	5,5	79,9	2,1	9,6	0,3	0,8					0,82
3	*P. echinatus*	1887	Barnardsvlei											0,2	1,6	5,5	82,5	1,5	7,1	0,4	0,7					1,27
4	*P. echinatus*	1937	Blydepoort		0,4	0,2							0,3	0,4	2,2	1.6	83,2	2,0	8,6	0,4	0,4					0,60
5	*P. echinatus*	1938	Blydepoort												0,3	1,9	96,4	0,2	0,8							3,29
6	*P. echinatus*	2141	Mariepskop		0,5	0,2									2,4	4,3	78,1	2,6	9,6	0,5	1,1		0,2			0,31
7	*P. echinatus*	2144	Mariepskop			0,2									2,3	2,3	78,1	1,9	13,1	0,9	0,8					0,52
8	*P. echinatus*	2146	Mariepskop										0,2		4,5	5,5	76,1	2,8	8,2	0,7	0,6	0,3	0,3	0,2	0,2	0,44
9	*P. echinatus*	2147	Mariepskop		0,2	0,3							0,3	0,2	4,3	2,0	68,6	2,5	17,4	0,8	1,7	0,4	0,4	0,3	0,3	0,31
10	*P. echinatus*	2149	Mariepskop		0,2										2,9	1,2	72,8	1,3	18,3	0,9	1,8					0,56
11	*P. echinatus*	2150	Mariepskop		0,5	0,4	0,2						0,2	0,3	2,2	8,7	68,8	2,3	12,7	1,2	1,6	0,2				0,34
12	*P. echinatus*	2151	Mariepskop										0,3	0,2	4,0	1,8	72,1	3,1	14,9	1,0	1,5	0,3	0,3			0,39
13	*P. echinatus*	2152	Mariepskop		0,2								0,2		3,3	1,7	62,4	12,1	17,1	0,5	1,8	0,2	0,3			0,38
14	*P. rostratus*	1642	Betty's Bay					0,2			0,2		0,8	1,3	3,2	41,0	29,5	14,5	6,8	1,9						0,18
15	*P. rostratus*	1643	Betty's Bay		0,3	0,3	0,6		0,4		0,3		0,7	1,4	3,7	12,0	65,9	3,3	9,7	0,3	0,5					0,22
16	*P. tricuspidatus*	1633	Tsitsikamma		0,2	0,2				0,2	0,2		0,4	0,6	3,4	3,9	67,9	3,1	17,1	1,7	0,9					0,26
17	*P. tricuspidatus*	1635	Tsitsikamma		0,2								0,2	0,3	2,3	2,1	73,0	2,7	16,3	1,4	1,1					0,32
18	*P. tricuspidatus*	1640	Betty's Bay				0,2		0,2		0,3	0,3	1,7	2,6	22,0	4,0	60,6	1,5	5,1	0,6	0,6					0,27
19	*P. tricuspidatus*	1641	Betty's Bay		0,3	0,4					0,2		0,7	1,2	6,0	4,8	72,3	4,1	6,9	1,4	0,9			0,2	0,2	0,18
20	*P. tricuspidatus*	1644	Betty's Bay		0,6	0,4		0,2	0,2		0,5	0,5	2,7	4,5	26,5	7,7	40,9	5,1	7,2	1,6	0,8					0,15
21	*P. tricuspidatus*	1711	Lamberts Bay		0,5				0,3		0,4	0,6	1,3	6,8	14,6	8,8	51,3	3,5	7,5	1,4	0,9			0,2	0,2	0,16
22	*P. tricuspidatus*	1715	Lamberts Bay	0,6	2,3	1,3	0,2		0,3	0,2	0,3		0,9	2,7	11,0	13,9	54,3	1,0	9,6	0,4	1,0					0,11
23	*P. tricuspidatus*	1718	Lamberts Bay		0,9	0,3	0,4	0,3	0,5	0,2	0,6		1,4	2,3	22,0	13,6	53,1		3,5	0,3	0,4					0,12

complete solubility of the long chain alkanes. The mixture was subsequently passed through a 5 × 5 mm silica gel G column and the column eluted with 1 mℓ of CCl_4. The total eluate was evaporated to dryness at room temperature under a stream of nitrogen. The residue was dissolved in 10 $\mu\ell$ CCl_4 and 1 $\mu\ell$ injected into the gas chromatograph. G.L.C. parameters: 3 mm × 2 m stainless steel column with 3 % SE-30 on Chromosorb 750, initial temp. 100 ° for 20 minutes, 3 ° rise per minute to 335 °, final period 60 minutes. N_2 flowrate 10 cm^3/minute, F.I.D.

Peaks were identified by co-chromatography with even numbered carbon chain length n-alkane standards and odd chain lengths by the straight line plot of absolute retention times against carbon number. To allow for possible changes in chromatographic parameters between analyses, retention times relative to C_{44} were also plotted and used for identification. Peak areas were obtained by triangulation.

Results

Table 1 illustrates the percentage of each n-alkane present in the samples. Only alkanes which are present at concentrations higher than 0,1 % are indicated, but even the lowest concentrations were taken into account in calculating the values, so that the values do not necessarily total 100 %.

All, except one of the sampled plants (*P. rostratus*, no. 14), have C_{29} as the largest constituent. In this and only one other additional plant (*P. tricuspidatus*, no. 20) is the total of all other alkanes more than 50 %. The domination of odd numbered carbon chain lengths as found in nearly all higher plants, is obvious. *P. rostratus* (no. 14) is highly unusual in that C_{28} is the dominant chain length. The absence of this obvious domination for the shorter chain lengths is probably to be found in the larger contribution of the ''internal'' alkanes to this fraction. These internal alkanes are known to have a ''flat'' distribution of chain lengths and to have a different composition from the ''external'' hydrocarbons (Herbin & Robins, 1969).

When the total alkane content of individual samples are plotted against the number of different chain length alkanes present in each sample (Figure 1), it is obvious that a negative correlation exists. The higher the amount of total alkanes, the lower the number of different chain lengths contributing to the total. The high total alkane content of samples are usually due to the presence of very large amounts (up to 96 %) of a single (C_{29}) chain length, with nearly all other fractions present in very low concentrations.

The disappearance of chain lengths other than the primary alkane may be due to the depletion of substrate materials during rapid synthesis of the waxes. This could lead to a rearrangement of existing alkanes to form the primary C_{29} alkane. If this is the case, it could be expected that only the ''internal'' hydrocarbons participate in this rearrangement, as the cuticular fraction cannot logically be expected to undergo such changes.

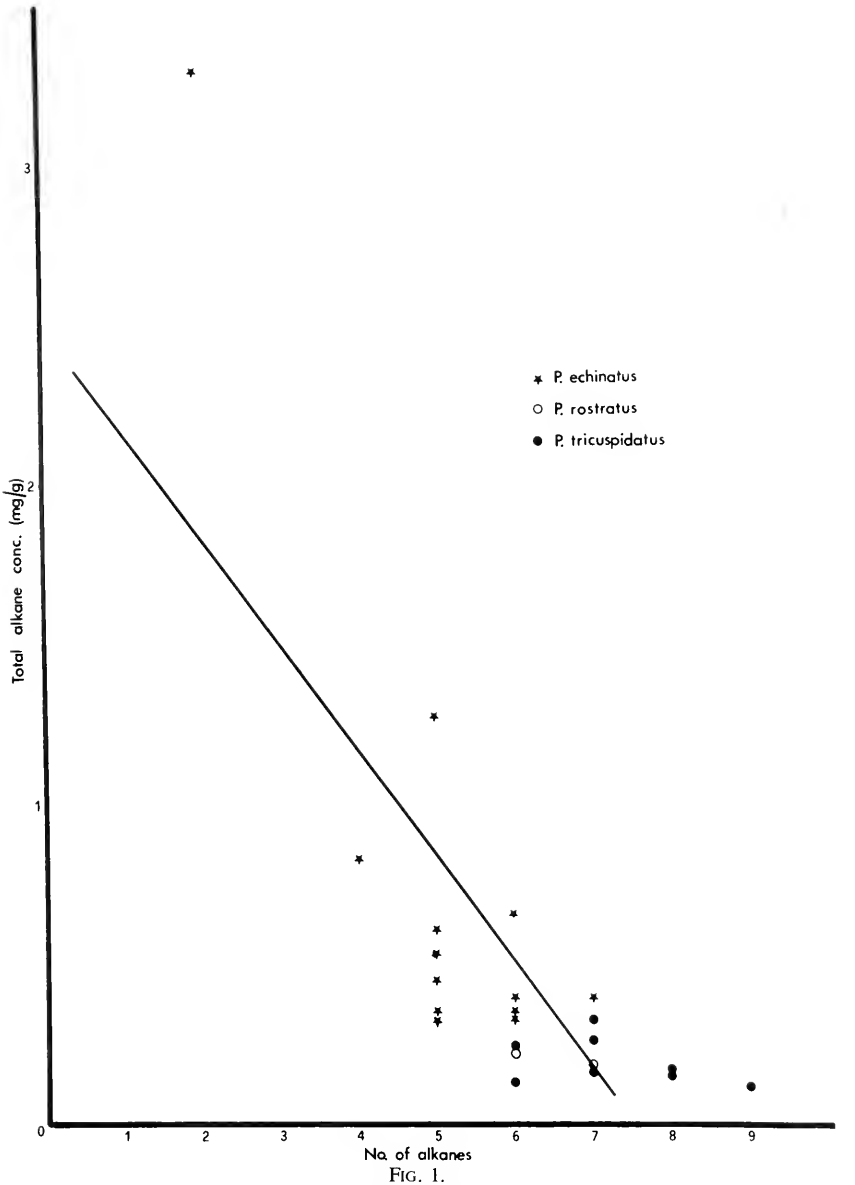

FIG. 1.
Negative correlation of −0,74 of total alkane content and number of alkanes found in each specimen. Linear regression line indicated.

The differences in alkane patterns observed in the studied samples cannot be ascribed primarily to environmental factors, as some of the plants with very different alkane compositions come from the same locality, as in case of the two specimens (nos. 4 and 5) of *P. echinatus* from Blydepoort and nos. 14 and 15 (*P. rostratus*) from Betty's Bay.

The alkanes of *Maytenus oleoides* and *Cassine eucleiformis* were also examined (results not given here) and the patterns proved to be very similar to those of *Pterocelastrus*. Variation of the patterns must therefore be due to genetic factors peculiar to each individual.

The data were processed with the aid of a number of numerical taxonomic computer programs, but all results showed that intraspecific variation is usually larger than the interspecific variation. No taxonomically valid deductions can thus be made from these results.

ACKNOWLEDGEMENTS

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CHANGES IN THE VEGETATION OF HLUHLUWE GAME RESERVE, ZULULAND, AS REGULATED BY EDAPHIC AND BIOTIC FACTORS OVER 36 YEARS

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Abstract

Examination of two sets of vegetation data showed a 5 % increase in the extent of Forest in the Reserve during the period from 1937 to 1974. A corresponding decrease of 8 % was found in the extent of Grassland. A considerable increase in the woody element of the vegetation at the expense of the herbaceous layer, particularly grasses, was evident even when allowance was made for a possible mapping error equivalent to one percent. These changes were mostly confined to upland areas and were ascribed to possible differences in burning treatments applied over the period. No significant changes were found in the areal extent of lowland communities where soils were primarily responsible for community distribution. However, soil erosion in the lowlands was ascribed to a reduction in herbaceous cover and, possibly, an increase of woody plants.

Uittreksel

VERANDERINGS IN DIE PLANTEGROEI VAN HLUHLUWE WILDRESERVAAT, ZULULAND, SOOS BEHEER DEUR EDAFIESE EN BIOTIESE FAKTORE OOR 36 JAAR

Die ontleding van twee stelle gegewens oor plantegroei het 'n toename van 5 % in die woudbedekking van die reservaat vanaf 1937 tot 1974 aangedui. Die omvang van grasveld het terselfdertyd met 8 % verminder. Die houtagtige komponente van die plantegroei het geweldig toegeneem ten koste van die kruidagtige laag, veral grasse, selfs met inagneming van 'n moontlike karteringsfout van een persent. Die veranderings was hoofsaaklik tot hoërliggende dele beperk en is aan moontlike verskillende brandbehandelings gedurende die tydperk toegeskryf. Geen beduidende verskille in die omvang van laerliggende plantgemeenskappe is gevind nie. Verspreiding van hierdie gemeenskappe is hoofsaaklik deur grondsoorte bepaal. Gronderosie in die laagliggende gebiede is egter aan 'n afname in kruidagtige bedekking en moontlik 'n toename in houtagtige bedekking toegeskryf.

Introduction

During 1936 Dr J. S. Henkel investigated the plant and animal ecology of the Hluhluwe Game Reserve, paying particular attention to possible relationships between the vegetation and breeding habits of tsetse flies. This work, done at the request of the Natal Provincial Council, was published together with a vegetation map in the following year (Henkel, 1937). A study of the same area by the author in 1973 aimed at producing vegetation information generally useful for management purposes, and the results were reported to the Natal Parks Board (Downing, 1974).

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This present paper aims to investigate, through a comparison of the 1937 and 1974 reports, the nature of any vegetation changes that might have arisen during the interval of 36 years.

Method

A first step was to relate the names of the various communities described in the two reports so that a single title could be allocated to each community. This was accomplished by reading of the two texts and comparison of the two vegetation maps. The eleven communities of the second report were thus reduced to correspond with the six communities mapped in the first report.

Copies of each of the two maps were made, and the separate areas representing the five communities were excised. The total area of each community was then estimated by means of an electronic planimeter; and the community areas were expressed as a percentage of the whole.

Visual comparisons of the distributions, shapes and areas were also made on intact copies of the maps in order to assess overall changes between the communities.

Results

Community Comparison

The results summarised in Table 1 show the relationships between communities, zones and regions in the two surveys. The number quoted for the mapping units of Henkel (1937) will be used as a simple way for referring to a community. Communities having a similar number were mapped as a single unit.

Most of the eleven communities described in 1974 were fairly easily related to the equivalent communities described in 1937. This was the case for Forest (unit 1), for Grassland and Parkland (unit 2). The Floodplain Grassland of 1974, not mapped separately in 1937, was incorporated as part of unit 2. The *Acacia-Ficus* Riverine Forest of 1974 corresponded with unit 5. The *Acacia burkei* Riverine Forest of 1974 was related to *Spirostachys* Parkland (unit 3) after environmental and distribution data were found to match. The *A. burkei* Closed Woodland was also accommodated, after matching, by unit 3. The remaining communities of 1974, comprising thicket and closed woodlands, were all similar to unit 4, the *Euclea-Combretum* Association of 1937. A problem arose from the *Dichrostachys-A. karroo* Association (unit 6) which was mapped separately in 1937 but which was included as part of the *Acacia* Wooded Grassland (unit 2) of 1974. Unit 6 was therefore included as part of unit 2. Thus were the eleven communities of 1974 related to five map units (reduced from six) of 1937.

TABLE 1.

A comparison of the communities and mapping units in Hluhluwe Game Reserve obtained by relating Henkel (1937) to Downing (1974).

Zone	COMMUNITIES OF HENKEL (1937)			COMMUNITIES OF DOWNING (1974)	
	Community name	Map Unit		Community name + map unit	Region
Humid Upland	Evergreen Closed Forest	Closed Forest	1	Forest	High-land
	Themeda Grassland	Grassland	2	*Themeda-Cymbopogon* Dry Grassland	
	Deciduous Parkland *A. caffra* + *Cussonia* sp.	Grassland	2	*Acacia* Wooded Grassland	
Inter-mediate	Parkland *A. nilotica* + *A. karroo* (with *Sclerocarya*)	Grassland	2	*Sclerocarya* Open Woodland	
—	—	—	2	Floodplain Grassland	Riverine
	Closed, Fringing, Riverine Forest	Riverine Forest	5	*Acacia-Ficus* Riverine Forest	
Dry Valley	Parkland of *Spirostachys* Tree Association (on silt)	Alluvial Sand	3	*Acacia burkei* Riverine Forest	
	Parkland of *A. burkei* Tree Association (on sand)	Alluvial Sand	3	*A. burkei* Closed Woodland	
	Euclea-Combretum Shrub Association	Scrub Lowlands	4	*Euclea* Thicket	Lowland
			4	*Combretum* Closed Woodland	
			4	*Spirostachys* Closed Woodland	
	Dichrostachys-A. karroo Shrub Association	Scrub Lowlands	6	(≡ *Acacia* Wooded Grassland)	

Change in Areal Extent

TABLE 2.

A comparison of the areas of communities mapped by Henkel (1937) at a scale of 1:31 543 and by Downing (1974) at a scale of 1:25 000 in Hluhluwe Game Reserve.

Unit	Type	1937		1974		% Change
		Area cm²	% Total	Area cm²	% Total	
1	Forest	191,62	12	415,85	17	+5
2 + 6	Grassland	748,40	49	984,04	41	−8
3	Alluvial Sand	81,99	6	243,16	10	+4
4	Lowland Scrub	436,11	28	594,34	25	−3
5	Riverine Forest	75,49	5	138,78	6	+1
—	Hluhluwe Dam	—	—	12,91	1	—
	Total	1 533,61	100	2 389,08	100	

Table 2 gives the results of planimetry and the estimated percentage increase or decrease in the areal extent of the communities between 1937 and 1974. The area of the Hluhluwe Dam is included at 1 % of the total. The Dam was built after 1960 and would have flooded roughly equal proportions of units 2 to 5 inclusive. The effects on the results are regarded as being almost negligible.

Riverine Forest (unit 5) shows a small increase of 1 %. This change is more likely due to technical error in map drafting than to any real change.

A 4 % increase in Alluvial Sand (unit 3) also seems mostly ascribable to a technical difference because the extensive *Acacia burkei* dominated stands mapped in 1974 as separate entities were added to unit 3. Fewer of these stands were separately mapped in 1937 and these were mostly regarded as part of the Lowland Scrub (see Henkel, 1937, p. 18 section 7). The 4 %, "false" increase of unit 3 is thus complementary to the 3 %, probably false, decrease of Lowland Scrub (Table 2, unit 4) which resulted from transfer of some *A. burkei* stands from the latter to the former during the 1974 survey.

The only real changes in areal extent would thus seem to be in the Closed Forest, which evidently increased by 5 %, and in the Grassland which evidently decreased by 8 %.

DISCUSSION

Initially, comparison of the 1937 and 1974 vegetation maps was attempted by optical enlargement of the former (at an original scale of about 1:31 543) to the 1:25 000 scale of the latter. This was abandoned because the two would not

match. The 1937 map was found to have a small distortion error, equivalent to 8 mm over the north-south distance of the map when compared to the 1974 map. Also, the shapes of some community boundaries were somewhat different, showing even a rotation through several degrees. The differences probably arose because Henkel, in the absence of any proper base map, had to survey the area *ab initio* by using a compass and aneroid barometer, both of which were also used to fix the vegetation boundaries. Small survey errors were likely to have resulted on occasions from magnetic deviations, as could be induced by dolerite outcrops, and by diurnal fluctuations in atmospheric pressure. Such errors were precluded from the 1974 map where topographic features were based on accurate sheets produced by the Trigonometric Survey; and where the distribution of community boundaries could, relatively easily, be seen on airphotos.

The errors in Henkel's work are nevertheless small, and the accuracy of his survey is quite remarkable considering the rather primitive instruments used. Henkel was invited to do the survey by the provincial government because he was known as a methodical and meticulous worker (Professor A. Bayer, pers. comm.)—a point confirmed by Table 3 which compares the spot heights obtained by Henkel (1937) with those obtained by modern survey. The maximum differences are by 100 feet, but with some only a few feet are involved. Similarly, the configurations of his contours, streams and rivers differ only slightly against the modern map. The vegetation data of Henkel, an experienced botanist and forester, can thus reasonably be expected to be rather accurate and reliable.

TABLE 3.

A comparison of altitudes (in feet) determined by Henkel (1937) in Hluhluwe Game Reserve as against altitudes given by recent Trigonometrical Survey on the South Africa 1:50 000 sheets.

Place	Altitudes in feet	
	Henkel	Trig. survey
Mthole (spot height)	1 524	1 529
Zangomfe (spot height)	1 135	1 141
Magwanxa	1 300	1 200
Sivivaneni	1 100	1 000
Umdindwana beacon	1 600	1 600

These expectations are confirmed by the closely similar extent of Riverine Forest, unlikely to change in area over time, which differed by only 1 % between 1937 and 1974. The narrow, fringing nature makes difficult delineation and measurement of Riverine Forest and, as mentioned previously, this difference is probably of a technical origin. An allowance of 1 % might thus be permitted for technical errors when comparing changes in the extent of the remaining communities—notwithstanding, of course, that a 1 % increase or decrease in

extent of a community over 40 years could be most important in conservation terms.

The increase of Alluvial Sand, and decrease of Scrub, in 1974 have already been explained in terms of differences in classificatory approach between the two authors, and as being mostly of a technical nature. Overgrazing, a cause of sparse grass cover and soil erosion, has sometimes been cause for concern in the Lowland Scrub during recent times. However, similar or fairly similar conditions prevailed earlier in the *Euclea* communities where Henkel (1937, pp. 16, 18) made the following comments.

(a) The grasses are so heavily grazed that there is not enough inflammable material to support a fire.
(b) Game animals seem very fond of these shrubby areas.
(c) The ground herbage is not abundant, particularly on hot aspects where much bare soil is exposed.

Henkel (1937) did not mention the presence of gullies which are nowadays conspicuous. The recent origin of many gullies is demonstrated by freshly exposed roots and toppled, but still living, trees near the gullies. Grass cover might thus have deterioriated a little since 1937.

A real increase in the extent of Closed Forest seems probable even if not as high as the 5 % given in Table 2. Henkel (1937, p. 22) mentioned that the dense, abrupt Forest margins were not damaged by fires which regularly burned through the adjacent Grassland and Parklands. However, Mr R. Porter (pers. comm.) has recently observed fire damage. Advances and retreats of margins at different localities, depending on the extent of fire immunity or damage at various localities from one year to the next, may well account for differences in the shapes of some Forest stands between 1937 and 1974.

Most stands of Forest occur on high hills, a topographic situation where the areal extent is exaggerated when studied on airphotos through a stereoscope. Such exaggeration was countered, as far as possible, during the 1974 study and any residual exaggeration should have been off-set by exaggeration from Grassland which also grows on the hills. An overall increase of Forest is, however, confirmed by the presence of a few, not previously mapped, fairly extensive stands of Forest as found south of Hlaza and N'kwanka Hills.

The extension of Forest has, logically, been at the expense of the adjacent Grassland which shows a decrease of 8 % in spite of several rather ''woody'' or ''wooded'' categories of the 1974 survey being included as part of the Grassland. Definition and classification is difficult for the vegetation series which covers the range from pure grassland, through varying degrees of woody establishment, to Savanna, Parkland, Open Woodland or even Thicket. Any equilibrium position on this series is often determined by a combination of fire behaviour and browsing (see Trollope, 1974). Changes in the effective interactions between these two factors and the vegetation probably account for the evident increase in the woody

element of Grassland and near-Grassland types in the Humid or Upland areas of the Reserve such that they are no longer classifiable as Grassland.

Both Henkel (1937) and Downing (1974) agreed that fire could determine the extent of the several communities in the Humid Upland Zone or Highland Region (units 1 and 2); and both authors emphasise the importance of edaphic factors in determining the extent of the various communities in the Intermediate and Dry Valley Zones (or Riverine and Lowland Regions) embracing units 3 to 6. The relative instability of the Highland communities is therefore not surprising because of the enormous variability possible in the kinds of fire treatment—let alone in the accompanying effects of grazing and browsing by herbivores in this Region. Similarly, the stability of the Riverine and Lowland communities is only to be expected because the nature of the soils is unlikely to change appreciably within many years. Some considerable increases in shrub density are, however, recalled by the late Professor A. W. Bayer (pers. comm.) who assisted Henkel.

Conclusions and Summary

1. In spite of some minor errors, equivalent to about 1 %, the vegetation survey of Henkel (1937) was sufficiently accurate for meaningful comparison with a survey based on modern methods.
2. Few, if any, boundary changes could be detected from communities in the Riverine and Dry Valley (or Lowland) zones although soil erosion may have accelerated in the Lowlands.
3. The shape of Forest patches has certainly changed over the last forty years, and fairly strong evidence indicates an overall increase in the extent of Forest.
4. The greatest change to have occurred is a decrease in the extent of Grassland and its replacement in many areas by woody categories.
5. The changes in Forest and Grassland are believed due to changes in the nature of fire/browsing interactions on the equilibrium between woody plants and grasses.
6. Relatively stable conditions in the Lowlands are maintained through edaphic control because the extent of each plant community is limited by a specific soil type.

Acknowledgements

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GERMINATION AND SEEDLING MORPHOLOGY OF *JUBAEOPSIS CAFFRA* BECC. (PALMAE)

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Abstract

Germination, which is remote-tubular, involves five steps. Firstly, the radicle appears through the germination pore in the endocarp. In stage two, lasting 10–12 days, the apocole grows downwards to an ultimate depth of 70 mm. Twenty days later, the apocole swells distally as the plumule enlarges in step three. Characteristic of stage four is the longitudinal splitting of the cotyledonary sheath followed by the emergence of the first scale leaf 43 days after stage one. A second scale leaf appears 12 days later. Three negatively geotropic lateral roots develop from the primary root. The appearance of the first eophyll, 80 days after the onset of germination represents the fifth step.

Growth of the seedling is slow and only seven foliage leaves are produced in the first 570 days. The first six are entire, lanceolate leaves while the seventh is initially bifid but later becomes irregularly pinnate with reduplicate pinnae to form the first typical compound leaf.

Uittreksel

ONTKIEMING EN SAAILING MORFOLOGIE VAN *JUBAEOPSIS CAFFRA* BECC. (PALMAE)

Ontkieming, wat verwyderd-buisagtig is, behels vyf stappe. Eerstens verskyn die radikula deur die kiemingsporie in die endokarp. In stap twee, wat 10–12 dae duur, groei die saadlobbuis afwaarts tot 'n maksimum diepte van 70 mm. Twintig dae later swel die distale gedeelte van die saadlobbuis namate die plumula vergroot. Kenmerkend van stap vier is die lengtespleet wat in die saadlobskede ontstaan namate die eerste skubblaar verskyn. 'n Tweede skubblaar volg na 'n verdere 12 dae. Drie negatief-geotropiese sywortels ontwikkel vanuit die primêre wortel. Die verskyning van die eerste loofblaar, 80 dae na die aanvang van kieming verteenwoordig stap vyf.

Groei van die saailing is stadig en slegs sewe loofblare word in die eerste 570 dae gevorm. Die eerste ses hiervan is gaafrandige, lineêre gelanseoleerde blare terwyl die sewende blaar aanvanklik tweespletig is, maar verander later na onreëlmatig geveerd met terugverdubbelde pinnas om die eerste tipiese saamgestelde blaar te vorm.

Introduction

Germination of palm seeds has been studied for nearly 400 years—the first recorded description being made in 1588 by Camerarius (Gatin, 1906) when he published his findings on the germination of *Phoenix dactylifera* seeds. Subsequent publications on this subject have been numerous but only a few relevant ones will be mentioned here.

In the monocotyledons, where plumular protection is a prerequisite for seedling development, the primary axis, with plumule and radicle is carried out of the

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seed into the soil by the cotyledonary sheath (Burtt, 1972). The extent to which the plant is removed from the seed varies from a few millimetres as in *Archontophoenix* to three metres or more in *Lodoicea* (Tomlinson, 1961).

Using previous systems (Richard, 1811 cited by Boyd, 1932; Martius, 1823–50 cited by Boyd, 1932) Gatin (1906), in a classic study of germination in 33 genera and 58 species of palms, described three basic germination types. The first type, remote-tubular, is exemplified by *Phoenix canariensis*, while the second, adjacent-ligular is found in *Archontophoenix cunninghamiana*. These two types are extremes while the third type, viz. remote-ligular germination, as seen in *Sabal umbraculifera*, is considered as an intermediate type. These three types are apparently comprehensive enough to accommodate all the other palms except possibly the genera *Nypa* and *Phytelephas* (Tomlinson, 1960a).

Germination of palm seeds is almost exclusively hypogeal (Tomlinson, 1960a; 1960b) except in one or two exceptional cases (Moore & Uhl, 1973). The cotyledon never becomes erect or expanded as a green assimilatory blade, but does possess the equivalent of leaf components, viz. lamina, petiole, leaf-sheath and sometimes a ligule (Tomlinson, 1961).

Very little literature is available on the germination of *Jubaeopsis caffra* seeds, and that which has been published is incomplete and, in some cases, questionable. This lack of information can be ascribed mainly to two facts. Firstly, *Jubaeopsis* grows naturally only in two very restricted and remote localities (Wicht, 1967; Robertson & Visagie, 1975) and consequently seeds are not freely available. Secondly, germination of the seeds is slow (up to a year) and the percentage germination is low (Robertson & Small, 1977).

Hill (1937) gives a brief description of *Jubaeopsis'* germination and states that the first leaf breaks through the cotyledonary sheath and expands above the ground. It can be concluded from this that germination is remote but not whether it is tubular or ligular. It would also seem that no scale leaves precede the first eophyll. In the light of Tomlinson's reports (1960a; 1960b) and that by Moore & Uhl (1973) this seems impossible.

Barry (1957) refers to the ". . . vertical descent of the hypocotyl to at least 18 inches below the surface of the soil . . ." in his report on *Jubaeopsis*. It is not clear whether the hypocotyl is borne down to this depth by the apocole or whether the hypocotyl itself elongates. This latter possibility is very unlikely.

Van der Schijff & Snyman (1970) equate the type of germination occurring in *Elephantorrhiza elaphantina* with that of the ". . . South African genera *Phoenix, Jubaea* and *Hyphaene* . . .". Apart from the fact that *Jubaea* is not indigenous to South Africa (Corner, 1966), the germination of this monotypic genus is remote-ligular while that of *Phoenix* is remote-tubular. It is not clear whether these authors are in fact referring to *Jubaea* or whether they actually mean *Jubaeopsis*.

The current information on germination of *Jubaeopsis* is thus very sketchy and

further, no data concerning seedling morphology and development are available. Consequently, it was deemed appropriate that these aspects be investigated fully.

Material and Methods

Seeds used in this study were obtained from a 43-year-old tree growing in St. George's Park, Port Elizabeth. Germination was hastened by maintaining the seeds at a moisture content of 14 % and incubating them in pure oxygen at 40 °C in the dark (Robertson & Small, 1977). Generally, germination is initiated within 21–30 days under these conditions.

Subsequent to the appearance of the radicle, the seedlings were planted in a mixture of soil, sand and peatmoss in 18 litre plastic containers and placed outside in semi-shade.

Results

(a) *Morphology of seed germination*

Five stages in the germination of *Jubaeopsis* seeds can be recognised.

Stage I: This stage is characterised by the appearance of the radicle and cotyledonary sheath or apocole through one of the three lateral germination pores in the endocarp of the nut. The manner in which the radicle tip emerges from the nut, varies. In some cases the pore lid is ruptured as the embryo breaks through it, while in other instances the intact lid is pushed off.

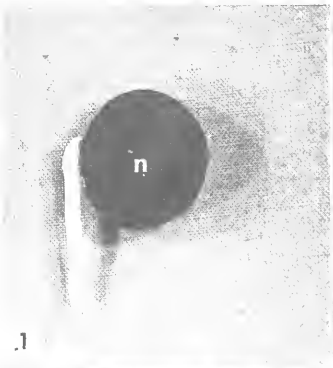
Immediately upon emerging from the nut, the apocole becomes positively geotropic.

Stage II: In this stage the apocole grows vertically downwards into the soil. The apocole is more or less of uniform thickness over its entire length, but has a sharp distal point (Fig. 1). Growth of the apocole is fairly rapid during this time and within 10–12 days from the onset of germination, reaches a length of approximately 50 mm.

Stage III: Thirty days after the appearance of the radicle from the nut, the distal section of the apocole starts to swell (Fig. 2). This phenomenon characterises Stage III and results from the development of the leaves in the plumule. At this point the apocole and radicle together are 80 to 100 mm long.

Stage IV: Stage IV is initiated by the longitudinal splitting of the cotyledonary sheath (Figs 3 and 4) as the volume of the plumule increases. Inside the nut the apex of the cotyledon has enlarged considerably during the preceding stages and a haustorium is formed (Fig. 5). This haustorium is the equivalent of a leaf lamina, while the middle piece of the cotyledon, i.e. between the haustorium and the split in the sheath, represents the petiole of a normal leaf. The section of the apocole which has split open, i.e. the cotyledonary sheath, can be equated with the typical leaf sheath found in the normal monocotyledonous leaf (Fig. 4).

At this time the proximal limit of the primary root is clearly demarcated (Figs 3, 4 and 6). Also characteristic of this stage and following shortly after the



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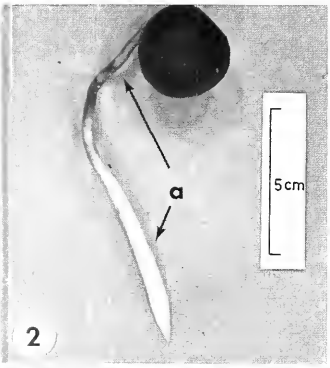

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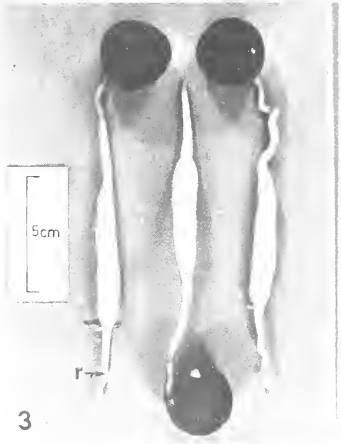

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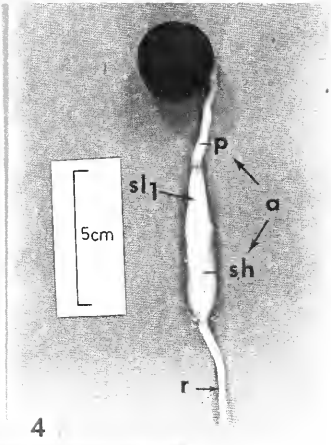

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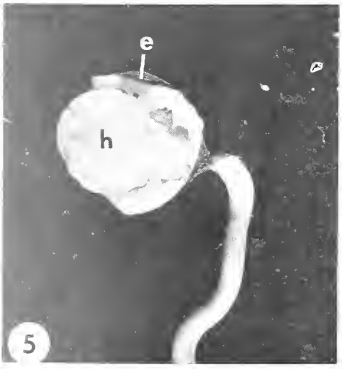

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initiation of the split in the cotyledonary sheath, is the development of lateral roots. The first lateral roots, of which there are three, emerge simultaneously and they are spaced evenly around the circumference of the primary root. These are not adventitious roots as they originate distally of the proximal limit of the primary root (Figs 6 and 7).

The first leaf to emerge from the split in the sheath is without a lamina and forms an entire sheath around the younger, developing leaves (Fig. 4). This occurs approximately 43 days after the onset of germination.

Twelve days later the second leaf emerges. This too is a needle-shaped leaf without a lamina and constitutes the second scale leaf (Fig. 7). Both scale leaves are rigid and have no trouble in piercing the soil.

At this stage the primary root is approximately 50 mm long and a number of small lateral roots have developed. These roots are very much smaller than the first three lateral roots which differentiated during Stage III. They are not restricted to any particular region of the primary root, but occur over most of its length and on the first three lateral roots as secondary lateral roots (Figs 6, 7 and 9).

The endosperm in the seed is almost entirely depleted at this stage and the cotyledonary haustorium completely fills the cavity which remains inside the endocarp. The rough nature of the haustorium surface results in the increased effectivity of this organ as an absorptive and digestive structure (Fig. 8).

Stage V: In this stage the first green foliage leaf or eophyll becomes visible (Fig. 9) and it is considered that this stage terminates germination as such and that it represents the first stage in the development of the seedling. This first green, bladed leaf appears 80–90 days after germination is initiated.

FIG. 1.
Stage II in germination of *Jubaeopsis caffra* seeds.

FIG. 2.
Characteristic swelling of apocole in Stage III.

FIG. 3.
Early Stage IV showing the split cotyledonary sheath.

FIG. 4.
Mid Stage IV—first scale leaf emerging.

FIG. 5.
Endosperm and haustorium in Stage III.

(a—apocole; e—endosperm; h—haustorium; n—nut;
p—petiole; r—radicle; sh—sheath; sl_1—first scale leaf).

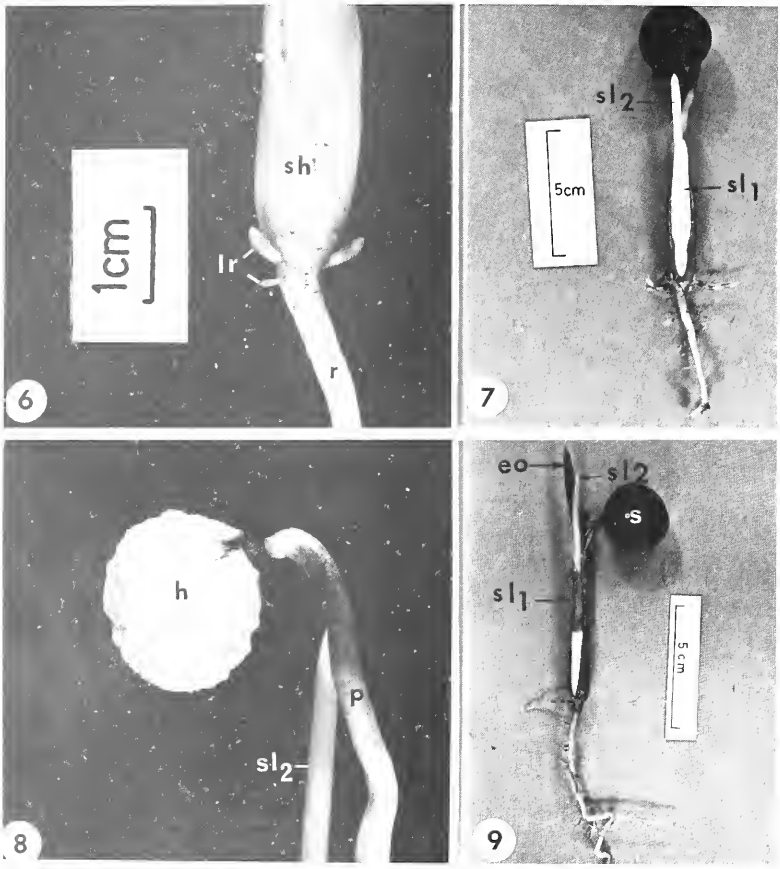


FIG. 6.
Development of first lateral roots during Stage IV.

FIG. 7.
Late Stage IV after emergence of the second scale leaf.

FIG. 8.
Haustorium during Stage IV.

FIG. 9.
Appearance of the first eophyll in Stage V.

(eo—eophyll; h—haustorium; lr—lateral roots; p—petiole; r—radicle; s—seed; sh—sheath; sl_1—first scale leaf; sl_2—second scale leaf)

(b) *Seedling Morphology*

Under experimental conditions, the growth of the *J. caffra* seedling is relatively slow and during the first 570 days of growth only seven eophylls are formed. The actual time of appearance of each of these foliage leaves, is presented in Table 1. No seedlings growing under natural conditions could be studied in this respect and it is thus not known whether the growth of this species is also as slow in its natural habitat as in the experiments.

TABLE 1.

Number of days between germination and the appearance of the first seven eophylls in *J. caffra*.

Eophyll	Days
1	80
2	180
3	280
4	360
5	390
6	540
7	570

The first six eophylls are all entire, linear lanceolate leaves about 400 mm long, the most obvious difference between them being in their width (Figs 10 and 11). The first eophyll attains a width of approximately 30 mm (Fig. 10), while the sixth one is more than 60 mm wide.

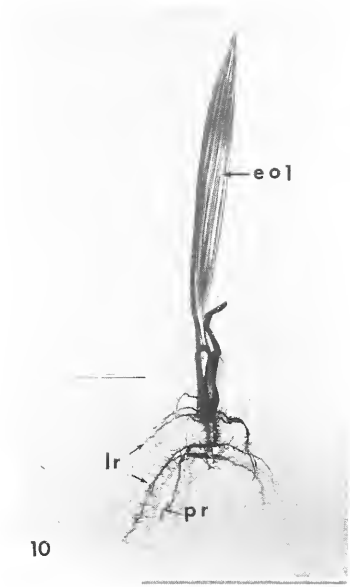
In *J. caffra* the seventh foliage leaf is irregularly pinnate (Fig. 12). The foliage leaves are clearly differentiated into segments which in the first six eophylls are not separated. Arrangement of these segments along the rachis is irregular, especially towards the apex of the leaf.

As the seventh foliage leaf appears, its apex is bifid. Subsequent development of this leaf does however result in the segments or leaflets tearing and separating. This separation does not occur in the more apically placed segments and consequently the apex of the seventh eophyll consists of two large, undivided leaflets in contrast to the smaller leaflets lower down on the rachis (Fig. 12).

Root development in the seedling phase is also relatively slow. One year after germination, i.e. at the time when the fourth eophyll becomes externally visible, the primary root is still functional, but it is supported in its activity by the three major lateral roots. These latter roots are nearly as well developed as the main root (Fig. 11).

DISCUSSION AND CONCLUSIONS

In view of the fact that the cotyledon is not extracted completely from the seed and that it does not expand above the ground and function as a photosynthetic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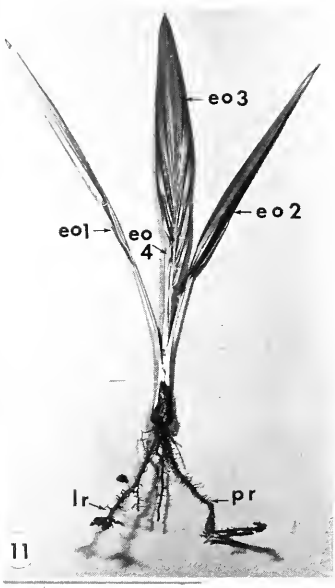
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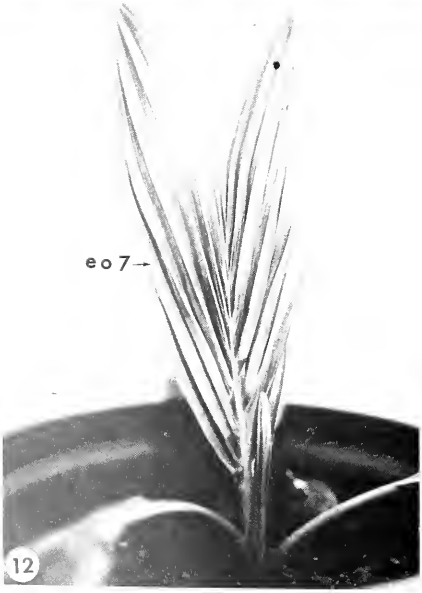
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organ, germination of *J. caffra* seeds is hypogeal. This is in accordance with the germination of all other palm species except *Nypa fruticans* (Tomlinson, 1960a, 1960b; Moore and Uhl, 1973).

Further, on the basis of the germination types described and defined by Gatin (1906) the seeds of *J. caffra* exhibit remote-tubular germination.

Apart from distinguishing between the types of germination, Gatin (1906) found that a correlation exists between the type of germination and the structure and orientation of the embryo concerned. In cases where the embryo is straight and the plumule and radicle lie in the same axis as the embryo, remote-tubular germination occurs. When the whole embryo is curved, germination is of the adjacent-ligular type, while remote-ligular germination takes place when the embryo is straight, but where the plumule and radicle lie obliquely to its longitudinal axis.

This general correlation for palms is true also in the case of *J. caffra* and its embryo is straight with the radicle and plumule lying in the same axis as the embryo.

The findings of this study in respect of the depth to which the apocole enters the soil, are contrary to those published by Barry (1957) who states that the hypocotyl descends to 18 inches (450 mm). It is clear from Fig. 9 that the apocole reaches a maximum length of approximately 70 mm.

Germination in other cocosoid palms varies extensively. In *Butia* (Boyd, 1932, *Elaeis* (Hussey, 1958) and *Cocos* (Corner, 1966) germination is adjacent-ligular. *Arecastrum* on the other hand exhibits remote-tubular germination (Gatin, 1906), while germination of *Jubaea* is remote-ligular (Gatin, 1906; Tomlinson, 1960a).

In view of the statements by Boyd (1932) and Moore & Uhl (1973), that remote germination is more primitive than the adjacent type and that the ligular types are more specialised than tubular germination, it would seem that *J. caffra*, with remote-tubular germination, is one of the more primitive cocosoid palms, while the closely related *Jubaea* is slightly more advanced. The coconut, *Cocos nucifera*, it appears, is somewhat more advanced in this respect than either of these two genera.

FIG. 10.
The first expanded eophyll of a *Jubeopsis* seedling (eo_1).

FIG. 11.
Three expanded, simple eophylls (eo 1–3) and the fourth (eo_4) unexpanded foliage leaf. All are entire, lanceolate leaves.

FIG. 12.
The seventh eophyll—irregularly pinnate (eo_7).

(lr—lateral roots; pr—primary root).

Two scale leaves are formed during germination and this number is always constant in *J. caffra*. It is usual for the number of scale leaves to be constant within any given species (Tomlinson, 1960b). However, the number varies from species to species, e.g. one each in *Livistona humilis* and *Phoenix roebelenii* and two in *Phoenicophorium borsigianum* (Moore & Uyl, 1973).

As far as the true foliage leaves are concerned, there exists a gradual transition from the first eophyll to the adult foliage leaf in palms generally (Corner, 1966). Tomlinson (1960a) has devised a classification system of six developmental patterns for the foliage of palms in respect of this transition from juvenile foliage to the adult leaf. The longest series of different eophyll forms as exhibited by *Roystonea* and *Stevensonia* represents the most primitive condition and includes entire, bifidous and pinnate juvenile forms.

The transitional series in the cocosoid palms while having a number of entire eophylls, which indicates a degree of primitiveness, also includes a number of more specialised irregularly pinnate transitional leaves. According to Tomlinson (1960a) this is indicative of a special evolutionary trend and consequently he considers the cocosoid palms as being anomolous in this respect.

Although it has been possible to observe the development of only the first seven eophylls of *J. caffra* during this study, it appears that *J. caffra* is similar to the other cocosoid palms in this connection.

When the radicle tip emerges from the germination pore, it is covered by a protective cap. Gatin (1906) states that the radicles of all palm embryos are protected in this manner and that the cap is in fact a radicular sheath originating from the cotyledonary tissue. This view is supported by Tomlinson (1960a). Von Guttenberg (1960) however rejects this interpretation and describes the cap as being nothing other than a primary root cap, originating from cell tiers in the proembryo which are totally different to the tiers which give rise to the cotyledon.

The results of this study, as well as those obtained from an earlier study of the embryogeny of *J. caffra* (Robertson, 1976) support this latter view and it is thus concluded that the radicular cap found in *J. caffra* is not of cotyledonary origin but that it is in fact a true calyptra originating from tier n′ in the fourth cell generation of the proembryo.

Gatin's (1906) division of germination into two phases, viz. a preparatory phase and a germinative phase is based primarily on the time at which the radicle emerges from the cotyledonary sheath. However, as discussed above, it appears that the radicle is not enveloped by the cotyledonary sheath and consequently the first organ to emerge from the germination pore is in fact the radicle with its rootcap. In view of this, it seems that in *J. caffra* germination consists of a germinative phase only.

In respect of lateral root formation in the seedling, it would seem that the condition found in *J. caffra* is different to that described by Gatin (1906) for other palms. Gatin states that where thick lateral roots are formed, only one is formed at

a time and that it takes over the function of the primary root. In *J. caffra* though, three thick lateral roots are formed simultaneously. Furthermore, the primary root is still functional two years after germination, so that it is in fact not immediately replaced by the thick lateral roots.

ACKNOWLEDGEMENTS

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CHLORIDE ABSORPTION BY ROOT, LEAF AND FLORAL TISSUES OF *PETUNIA*

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Abstract

Chloride absorption by root, leaf and floral tissues of *Petunia* was compared at two temperatures (30 and 2 °C), employing different absorption periods, and in the presence and absence of a desorption treatment. All treatments revealed highest absorption by floral tissue. This was further confirmed by the absorption of chloride by the various tissues from solutions in the low (0–1 mM) and high (1–50 mM) concentration ranges.

The results offer a possible explanation for the observed effects of organic and inorganic solutes on the longevity of cut flowers.

Uittreksel

CHLORIEDOPNAME DEUR WORTEL-, BLAAR- EN BLOMWEEFSEL VAN *PETUNIA*

Die opname van chloried deur wortel-, blaar- en blomweefsel van *Petunia* is by twee temperature (30 en 2 °C), met verskillende tydperke van opname en met en sonder 'n desorpsiebehandeling vergelyk. By alle behandelings is die hoogste opname met blomweefsel verkry. Dit is verder bevestig deur die opname van chloried deur die verskillende weefsels uit oplossings in die lae (0–1 mM) en hoë (1–50 mM) konsentrasiegebiede.

Die resultate bied 'n moontlike verklaring vir die waargenome effek van opgeloste organiese en anorganiese stowwe op die houvermoë van snyblomme.

Introduction

Halevy and Mayak (1974) observed that treatments to improve the quality and longevity of cut flowers frequently have the effect that the foliage leaves desiccate. The lack of data on the uptake of solutes by floral tissue was strongly emphasised by Halevy (pers. comm.).

Borohov, Tirosh and Halevy (1976) obtained lower values for ABA content and water deficit in petals of sucrose-treated flowers than in controls. They concluded that the effect of sucrose on the ABA content of the petals was at least partly due to its effect on changes in water deficit in the petals.

In the present study, a comparison was made of the uptake of chloride by root tips, leaf discs and discs of the petals of *Petunia*.

Material and Methods

Seedlings of *Petunia* x Hybrida obtained from a local nursery were placed in 3 ℓ containers filled with half-strength culture solution—solution No. 1 of Hoagland and Arnon (1938), in which Fe-EDTA was used as the Fe source. The plants were

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allowed to grow for two weeks, after which they were transferred to full-strength culture solution. At first the culture solutions were renewed fortnightly, but later at weekly intervals. The solutions were replenished with deionised water daily and continually aerated.

The plants were cultivated in a growth chamber, with a daily photoperiod of 14 h (28 ± 2 °C) and light intensity of c. 7 000 lux—until they were flowering profusely. At this time experimental material was obtained as follows: discs, 5 mm in diameter, were cut from the youngest fully mature foliage leaves as well as from the petals of fully open flowers, and the apical 10–15 mm segments of the roots were excised, and immediately placed in 0,5 mM $CaSO_4$ solution. Foliage leaf and petal samples consisted of at least 50 and 80 discs respectively; samples of root tissue had a fresh mass corresponding to 50 leaf discs (c. 0,5 g).

The tissue samples were placed in nylon gauze bags, and immersed in a second 0,5 mM $CaSO_4$ solution at 30 °C for one hour, before they were transferred to the experimental solutions, in which their chloride uptake was to be studied.

Two experiments were conducted. In the first, the uptake of chloride was studied at 30 and 2 °C, with and without a desorption treatment. The experimental solution contained 0,5 mM KCl, labelled with ^{36}Cl, and 0,5 mM $CaSO_4$. The desorption medium was identical to the experimental solution, except for the ^{36}Cl, and was kept at 2 °C. Following absorption periods of 10, 30 and 60 minutes, at 30 and 2 °C, half of the samples were subjected to a desorption treatment of 30 minutes.

In the second experiment the chloride concentration varied from 0,02 to 50 mM, thereby including both so-called "low" and "high" concentration ranges. All solutions contained KCl, labelled with ^{36}Cl, in 0,5 mM $CaSO_4$. Each desorption solution had the same chloride content as the experimental solution, was also made up with 0,5 mM $CaSO_4$ solution and was kept at 2 °C, but did not contain ^{36}Cl. At each chloride level an absorption period of one hour was followed by a desorption period of 30 minutes.

Following the absorption periods in the different experimental solutions, each sample was rinsed for a total of one minute in a series of four beakers, each containing 200 mℓ deionised water. For the desorption treatment, the samples were transferred (after rinsing) to the desorption solution, following which they were rinsed again as above.

After a brief drying period (too dry material was difficult to remove from the nylon gauze bags) the tissues were placed in scintillation vials and suspended in 5 mℓ Insta-gel (Packard Instrument Co.), and radioactivity determined by means of a Beckman LS–133 scintillation system. The amount of absorbed chloride was subsequently calculated.

At least two replicates of each treatment were employed. In view of the very high degree of uniformity in the data, calculation of the standard error was not considered necessary.

TABLE 1.

Effect of temperature, desorption treatment and length of absorption period on the chloride content of root, leaf and floral tissues of *Petunia*. (Experimental solution contained 0,5 mM KCl (labelled with ^{36}Cl) and 0,5 mM $CaSO_4$. Desorption solution contained 0,5 mM KCl and 0,5 mM $CaSO_4$. Desorption period: 30 minutes at 2 °C. Results represent the average of 2 replicates.)

Absorption period (min.)	Chloride content ($\mu g\ g^{-1}$ fresh mass)			
	30 °C		2 °C	
	No Desorption	Desorption	No Desorption	Desorption
	Root tissue			
10	3,42	1,85	0,58	0,15
30	7,23	5,43	0,75	0,34
60	13,74	9,68	1,05	0,62
	Leaf tissue			
10	0,58	0,12	0,36	0
30	1,29	0,63	0,39	0,16
60	1,49	1,61	0,56	0,28
	Floral tissue			
10	3,57	2,67	1,16	0,25
30	11,91	10,76	2,60	0,51
60	23,28	16,82	3,65	1,62

TABLE 2.

Chloride content of root, leaf and floral tissues following absorption at 2 °C, as a percentage of that following absorption at 30 °C.

Absorption period (min.)	No Desorption	Desorption
	Root tissue	
10	17,0	8,1
30	10,4	6,3
60	7,6	6,4
	Leaf tissue	
10	62,2	0
30	30,2	25,4
60	37,6	17,4
	Floral tissue	
10	32,5	9,4
30	21,8	4,7
60	15,7	9,6

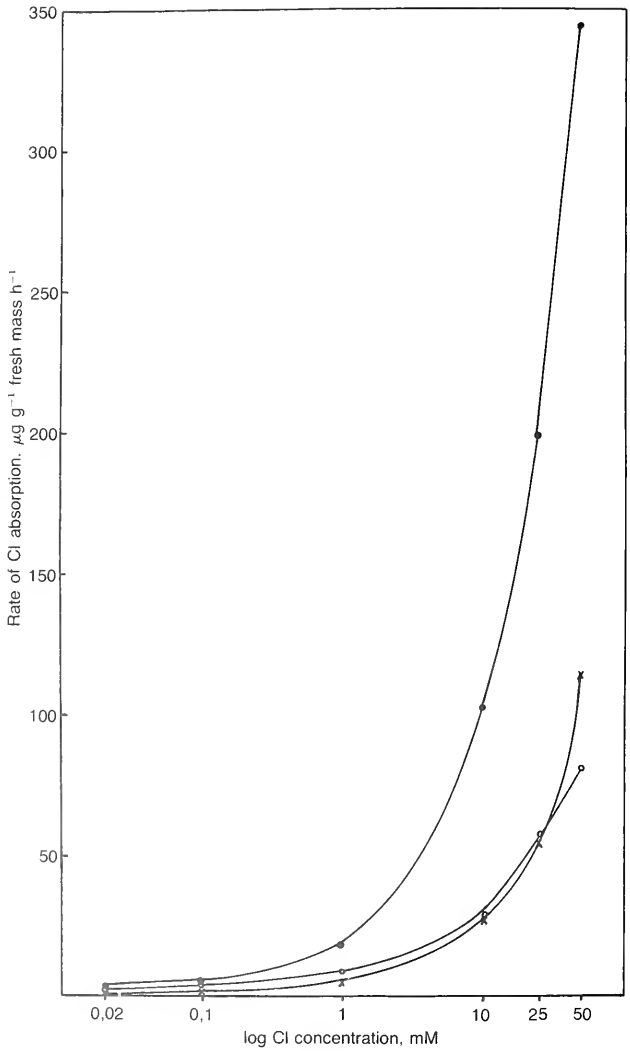

FIG. 1.

Rate of chloride absorption by root (○——○), leaf (x———x) and floral (●——●) tissues in the low (0,02–1 mM) and high (1–50 mM) concentration ranges. Chloride supplied as KCl (labelled with ^{36}Cl) in 0,5 mM $CaSO_4$ solution. Absorption period: 1 h at 30 °C, followed by desorption for 30 minutes in solutions of KCl plus $CaSO_4$ at 2 °C.

Results and Discussion

Of the three different tissues under investigation, the petal discs absorbed chloride at the highest rate whilst the foliage leaf discs did so at the lowest rate (Table 1). The depressing effect of low temperature on chloride absorption is apparent in all instances, but is better illustrated in Table 2. In Table 2, the high values for foliage leaf tissue compared to root and petal tissues where no desorption treatment was employed (i.e. measuring both metabolic and passive components of absorption), are perhaps indicative of a greater passive component in the uptake of chloride by foliage than by the other tissues.

Any doubt about the greater absorption ability of petal tissue as compared to root and foliage leaf tissues, is ruled out by the absorption curves in Figure 1. The root tips and foliage leaf discs absorbed chloride at virtually the same rate in all the treatments except at the highest chloride concentration where the foliage leaf discs yielded higher values than the root tips. Uptake by petal tissue greatly exceeded that of the other two tissues at all concentrations above 0,1 mM. This suggests that chloride absorption by the petal discs is largely an active process.

These findings might help to explain the fact that longevity of cut flowers is prolonged by certain organic and inorganic solutes, whereas the foliage leaves frequently desiccate under these conditions. Active solute absorption by petal tissue would bring about a lowering of water potential, stimulating water absorption, whereas a high concentration of solutes in the free space of foliage leaf tissue, not accompanied by the same degree of active absorption, would actually induce the reverse effect—an outward movement of water, leading to desiccation.

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NOMENCLATURAL NOTES ON SOUTH AFRICAN CRUCIFERAE

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Abstract

Thirty-five taxa of South African Cruciferae previously described by O. W. Sonder are typified by specimens from Sonder's herbarium in the Swedish Museum of Natural History, Stockholm (S). *Heliophila viminalis* E. Mey. ex Sond. is added to the synonymy of *H. digitata* L. fil. *H. thunbergii* Steud., with two varieties, var. *thunbergii* and var. *macrostylis* (E. Mey. ex Sond.) B. Nord., comb. nov., has been substituted for the former name *H. latisiliqua* E. Mey. ex Sond.

Uittreksel

AANTEKENINGE OOR DIE NOMENKLATUUR VAN SUID-AFRIKAANSE CRUCIFERAE

Vyf-en-dertig taksa Suid-Afrikaanse Cruciferae, voorheen deur O. W. Sonder beskryf, word getipeer deur eksemplare vanuit Sonder se herbarium in die Sweedse Museum vir Natuurwetenskap in Stockholm (S). *Heliophila viminalis* E. Mey. ex Sond. word by die sinonieme van *H. digitata* L. gevoeg. *H. thunbergii* Steud., met twee variëteite, var. *thunbergii* en var. *macrostylis* (E. Mey. ex Sond.) B. Nord., comb. nov., vervang die voormalige naam *H. latisiliqua* E. Mey. ex Sond.

The South African herbarium of O. W. Sonder, the renowned co-author of *Flora capensis* (Harvey & Sonder, 1860–65), was acquired by the Swedish Museum of Natural History (S) in 1875. In the museum archives I recently came across the purchase contract, signed by Sonder and by N. J. Andersson, the Curator of the Botany Dept. at that time (Fig. 1). Further details of the transaction will be presented elsewhere (Nordenstam, in press). The important fact, stressed again here, is that most of the types of Sonder's South African taxa are now to be found in the Stockholm herbarium (S). The Sonder material in the herbaria at Melbourne (MEL) and Lyon (LY) (cf. Stafleu, 1967: 193), is of only secondary importance, since it consists mainly of fragments, duplicates and of material collected together by Sonder later than 1875.

The supposition that Sonder retained bits and pieces of the material of many of the species in 1875, when his South African herbarium was shipped to Stockholm (Nordenstam, in press), receives some support when a comparison is made between Sonder's *Heliophila* illustrations (1846) and the specimens on which they were based (Figs 2–3). Most of these specimens are now to be found in Stockholm, but in several cases branches, or other pieces, have obviously been removed at some time (cf. Fig. 3C, D).

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Von Herrn Dr. W. Sonder in Hamburg kaufe ich Endesunterschrieben für Rechnung der Academie der Wissenschaften in Stockholm:

Das Herbarium der Flora Capensis, in dem ganzen Umfange wie es für die Flora Capensis vorgelegen hat, und mit sämmtlichen vorhandenen Doubletten unter folgenden Bedingungen.

1, am heutigen Tage, den 28 August 1875 bezahle ich 2500 Schwedische Kronen durch einen Wechsel von Lst 2809,- auf Johannes Schubach & Söhne in Hamburg, heute fällig.

2, Den anderen Theil der Kaufsumme bezahle ich in fol-gende Summen; am 1 Juni 1876 entrichte ich achthundert schwed. Kronen; ferner am 1 Juni 1877 wiederum 800 schwed. Kronen, und den Rest mit 800 schwed Kronen am 1 Juni achtzehnhundert acht und siebenzig.

3, Dagegen verpflichtet sich Dr W. Sonder die ganze, vollständige Sammlung verpackt, und mit Angabe des Inhalts, dem von mir ihm genannten Spediteur in Hamburg zu überliefern.

4, Herr Dr W. Sonder verspricht, falls er sich in den folgenden Jahren afrikanische Pflanzen aus dem Gebiet der Flora Capensis durch Tausch oder sonst zu kommen sollten, sofern sie ein besonderes Interesse für das gegenwärtig verkaufte Herbarium besitzen, dem Museum in Stockholm zu kommen zu lassen.

Solches ist verabredet und beschlossen und von beiden Contrahenten eigenhändig unterschrieben.

Hamburg
d. 28 August 1875.

N. J. Andersson
Dr W. Sonder

Unfortunately, the fact that Sonder's South African herbarium is now located in Stockholm is not generally known. For example, Marais' meritorious treatment of the family Cruciferae for the *Flora of Southern Africa* (Marais, 1970) was prepared without any recourse to Sonder's original material in the Stockholm herbarium. At best, isotypes in other herbaria were cited as types.

In the present study, Sonder's taxa of South African Cruciferae (Sonder, 1846, 1850, 1860) are typified by specimens present in Stockholm (holo- or lectotypes), and some nomenclatural changes are proposed. The taxa are arranged in the sequence of *Flora capensis* Vol. 1 (Sonder, 1860).

1. **Matthiola stelligera** Sonder (1850: 1)

Syntypes: Lesotho, N of Caledon River, Oct. (''114.10''), *Zeyher* (S, lecto.!); near Orange River, between Kraairivier and Witbergen, Sept. (''118.9''), *Zeyher* (S!).

The two syntypes are mounted together on one sheet. In *Flora capensis* Sonder (1860) reduced the taxon to a variety of *M. torulosa* (Thunb.) DC. (var. *tricornis* Sond.), a variety which is no longer recognised (Marais, 1970).

2. **Nasturtium caledonicum** Sonder (1850: 2)

Type: Caledon River, *Zeyher 21* (S, holo.!).—Marais cited only isotypes in BM, K and PRE.

At the same time Sonder also described *N. fluviatile* E. Mey. ex Sond. He later degraded *caledonicum* to a mere variety of the latter species (Sonder, 1860). The name currently adopted is *Rorippa fluviatilis* (E. Mey. ex Sond.) Thell., with two varieties, var. *fluviatilis* and var. *caledonica* (Sond.) Marais (1970).

Fig. 1.

The purchase contract, in Sonder's hand-writing, regarding the sale of Sonder's South African herbarium in 1875 to the Swedish Museum of Natural History, which at that time was under the auspices of the Swedish Academy of Science. The text reads:

''Von Herrn Dr W. Sonder in Hamburg kaufe ich Endesunterschreiber für Rechnung der Academie der Wissenschaften in Stockholm:

Das Herbarium der Flora Capensis, in dem gansen Umfange wie es für die Flora Capensis vorgelegen hat, und mit sämmtlichen vorhandenen Doubletten unter folgenden Bedingungen:

1, am heutigen Tage, den 28 August 1875 bezahle ich 2 500 Schwedische Kronen durch einen Wechsel von R[eichsmark] 2809.–, auf Johannes Schuback & Söhne in Hamburg, heute fällig.

2, Den anderen Theil der Kaufsumme bezahle ich in folgenden Terminen: am 1 Juni 1876 entrichte ich achthundert schwed. Kronen; ferner am 1 Juni 1877 wiederum 800 schwed. Kronen, und den Rest mit 800 schwed. Kronen am 1 Juni achtzehnhundert acht & siebenzig.

3, Dagegen verpflichtet sich Dr W. Sonder die ganze vollständige Sammlung verpackt, und mit Angabe des Inhalts, dem von mir ihm genannten Spediteur in Hamburg zu überliefern.

4, Herr Dr W. Sonder verspricht, falls ihm in den folgenden Jahren afrikanische Pflanzen aus dem Gebiet der Flora Capensis durch Tausch oder sonst zukommen sollten, sofern sie ein besonderes Interesse für das gegenwärtig verkaufte Herbarium besitzen, dem Museum in Stockholm zukommen zu lassen.

Solches ist verabredet und beschlossen und von beiden Contrahenten eigenhändig unterschrieben.

Hamburg d. 28 August 1875 Dr N. J. Andersson Dr W. Sonder''

3. **Turritis dregeana** Sonder (1850: 2)

Type: Witbergen (locality given by Sonder, l.c., not on the sheet), Jan., *Drège 7537* "a" (S, holo.!).

Now thought to be conspecific with *Arabis glabra* (L.) Bernh. (syn. *Turritis glabra* L.) and to have been introduced into South Africa.

4. **Arabis ? nudiuscula** E. Mey. ex Sonder (1860: 22, sphalm. *"nudicaulis"*, but corrected in the "Addenda and Corrigenda", p. 19*)

Type: Graafreynet, Zondag River, Sneeuwbergen etc., *Drège* "a" (S, lecto.!). Fig. 4 D.

Marais (1970) adopted the name *Rorippa nudiuscula* Thell. and selected a *MacOwan* collection as the lectotype, regarding this as a description of a new species rather than a new combination. However, the fact that Thellung was doubtful of the identity of his material is irrelevant as regards the validity of his combination, which must be accepted as valid. Accordingly, the correct name is *R. nudiuscula* (E. Mey. ex Sond.) Thell., with lectotype as indicated above.

5a. **Sisymbrium capense** Thunb. var. **latifolium** Sonder (1860: 24)

Syntypes: Albany, between Vishrivier and Fort Beaufort, *Drège, "Sisymbrium argutum* E. Mey. b" (S, lecto.!); Uitenhage, Zwartkopsrivier, *Ecklon 191* (S!), *Zeyher 1893 b* (S!); Swellendam, Kenko River, *Zeyher 1893* (S!); Port Natal, *Gueinzius 517* (S!); *Thunberg, Sisymbrium strigosum fol. e* (UPS).

5b. **Sisymbrium capense** Thunb. var. **montanum** Sonder (1860: 24)

Type: Sneeuwbergen, between Compassberg and Rhinosterbergen, *Drège, "Sisymbrium montanum* E. Mey. b" (S, lecto.!).—The locality "Vische River" given by Sonder (l.c.) is probably a mistake.

5c. **Sisymbrium capense** Thunb. var. **angustifolium** Sonder (1860: 24)

This explicitly includes the type of *S. capense* Thunb. and is thus illegitimate under the present rules, the correct name being var. *capense*.

Marais (1970) did not recognize any varieties of the widespread species, *S. capense* Thunb.

6. **Sisymbrium exasperatum** Sonder (1850: 3)

Type: Sandrift, Orangeriver, *Zeyher 18* (S, holo.!)

Sonder possessed the unicates of Drège, Ecklon and Zeyher (cf. Nordenstam, in press), and this specimen is one of them, as is clearly stated on the label.

Sonder misinterpreted the type of pubescence, which actually comprises both simple and branched hairs, and the species is now regarded as a synonym of *S. burchellii* DC.

7. **Lepidium myriocarpum** Sonder (1850: 4)

Type: Bathurst, Glenfilling, *Drège 7541* "aa" (S, holo.!). Marais (1970) cited only the isotypes in BM, K and PRE.

This rare species is represented in the Stockholm herbarium also by *Zeyher 24* from Caledon River. This specimen is cited in *Flora capensis*, but not in the original description, and is accordingly not a syntype.

8. **Lepidium linoides** Thunb. var. **pumilum** Sonder (1860: 28)

Type: Winterveld, between Nieuwjaarsfontein and Ezelsfontein, *Drège 9501* (S, holo.!).

This taxon is now included in *L. ecklonii* Schrad. (Marais, 1970).

9. **Lepidium trifurcum** Sonder (1850: 4)

Type: Bechuanaland, Modderriver, *Zeyher 23* (S, holo.!). Fig. 4G.

Marais (1966, 1970), who examined the isotypes in K and PRE, reduced the taxon to a subspecies of *L. divaricatum* Ait., but Jonsell (1975: 37) restored its specific status.

10. **Lepidium hirtellum** Sonder (1860: 30)

Type: Uitenhage, Quaggasvlakte, *Ecklon & Zeyher 45* (S, holo.!). Fig. 4F. Marais only saw an isotype in LE.

This species is now included under *L. ecklonii* Schrad. (Marais, 1970).

11. **Brachycarpaea laxa** (Thunb.) Sond. var. **stricta** Sonder (1860: 33)

Type: Between Pedroskloof and Leliefontein, *Drège 7584* "c" (S, lecto.!).

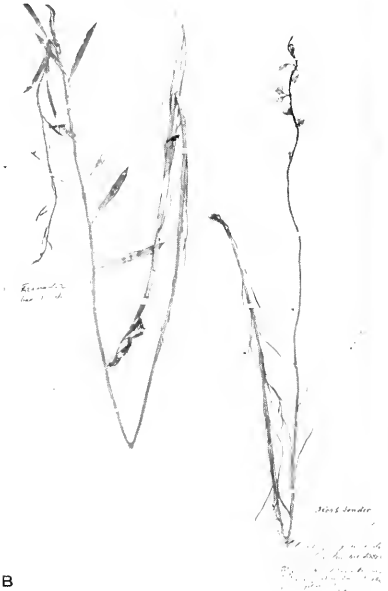
This is now one of the synonyms for *B. juncea* (Berg.) Marais (1970).

12. **Cycloptychis polygaloides** Sonder (1860: 34)

Type: Tulbagh, *Zeyher* (S, holo.!). Fig. 4E.

The correct name is *Heliophila nubigena* Schltr (Marais, 1970).

A Heliophila rigidiuscula Sond



B

Tab XXVII

C Heliophila cornuta Sond

D

13. **Heliophila affinis** Sonder (1846: 208)

Syntypes: Vorberge der Camisbergen, 20.VIII.1830, *Drège* (S, lecto.!); Haazenkraalsrivier, "*Helioph. longifolia* DC. b" (S!); between Uitkomst and Geelbekskraal, *Drège* (K).

14a. **Heliophila amplexicaulis** L. fil. var. **grandiflora** Sonder (1860: 40)

Type: Wupperthal, *Drège 7551* leg. *v. Wurmb* (S, holo.!).

14b. **Heliophila amplexicaulis** L. fil. var. **spathulata** Sonder (1860: 40)

Type: Vorberge der Camisbergen etc., *Drège* (S, holo.!).

Marais (1970) did not recognize any infraspecific taxa of *H. amplexicaulis* L. fil.

15. **Heliophila concatenata** Sonder (1846: 214)

Type: Paarlberg, *Drège 7576* "a" (S, holo.!).

As conceived by Marais (1970), this represents a difficult and insufficiently investigated complex.

16. **Heliophila monticola** Sonder (1846: 216)

Type: Mierenkasteel, *Drège, "Helioph. pendula* W." (S, holo.!). Fig. 4C.

Now one of the synonyms for *H. variabilis* Burch. ex DC.

17. **Heliophila dentifera** Sonder (1846: 219)

Type: Devils Mt., *Ecklon & Zeyher* (S, holo.!).

Marais (1970) united this taxon with *H. meyeri* Sond., adopting the latter epithet.

18. **Heliophila flacca** Sonder (1846: 223)

Type: Caledon Baths, Zwarteberg, *Ecklon & Zeyher* (S, lecto.! iso.!), *Zeyher 1894* (S!).

This taxon was reduced by Marais (1966, 1970) to *H. diffusa* (Thunb.) DC. var. *flacca* (Sond.) Marais. Apart from the typical variety, he also included *H.*

FIG. 2.
Sonder's illustrations and the original specimens of *Heliophila rigidiuscula* Sond. (A, B) and *H. cornuta* Sond. (C, D).

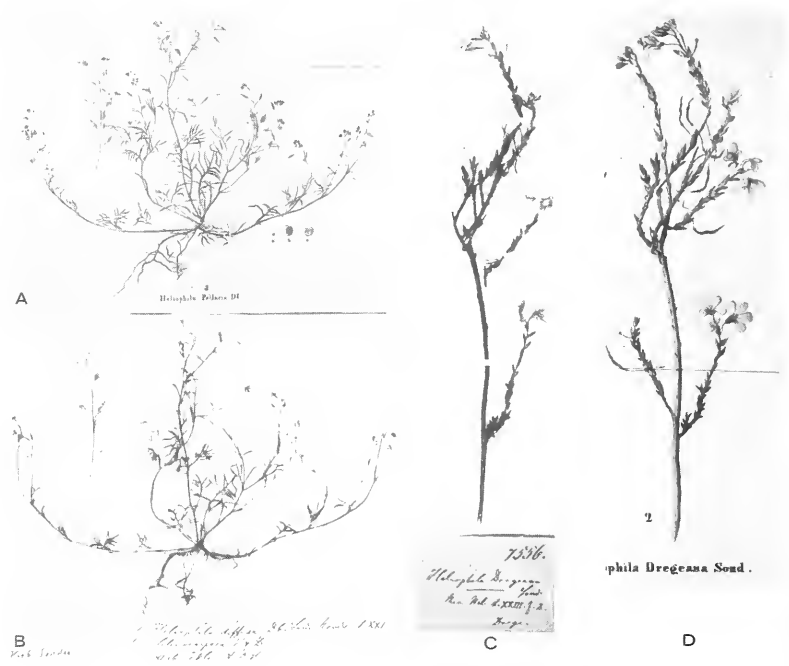


FIG. 3.
Sonder's illustrations and the original specimens of *Heliophila peltaria* DC. (A, B) and *H. dregeana* Sond. (C, D). Note the erroneous name (''*Heliophila diffusa*'') written by Sonder against specimen B. Furthermore, note the missing branches on specimen C.

peltaria DC. in var. *diffusa*. Sonder had kept *H. diffusa* and *peltaria* separate (a decision which was also followed by Adamson in the *Flora of the Cape Peninsula*) and illustrated both species in his revision of the genus (Sonder, 1846). Oddly enough, however, he mixed up the two taxa in his own herbarium, annotating all specimens of *diffusa* as *peltaria*, and vice-versa (cf. Fig. 3A, B).

19. **Heliophila latisiliqua** E. Mey. ex Sonder (1846: 224)

This was based on *Lunaria elongata* Thunb. and is accordingly typified by a Thunberg specimen in Uppsala (no. *14957 p.p.)*, not by *Drège 585* as stated by Marais (1966, 1970). Sonder did not adopt Thunberg's specific epithet, because of the existence of *H. elongata* (Thunb.) DC., which is a different taxon.

Carpopodium thunbergii E. & Z. (Ecklon & Zeyher 1834–35) is an earlier synonym, but an illegitimate one, since under that generic name Thunberg's

epithet *elongata* should have been adopted. Steudel (1841) combined the epithet *thunbergii* of Ecklon & Zeyher under *Heliophila*, which under the present rules should be regarded as the publication of a new name, not a new combination (Art. 72 Note 1 in the Code). Furthermore, Steudel also cited *Lunaria elongata* Thunb. as a synonym, so there is no doubt about the validity of his new name. *H. thunbergii* Steud. thus takes precedence over *H. latisiliqua* Sond., and its two varieties (Marais, 1966, 1970) must be re-named as follows.

(a) **H. thunbergii** Steud. var. **thunbergii**
Lunaria elongata Thunb., Prodr.: 107 (1800). Type, see above. *Carpopodium thunbergii* E. & Z. (1834–35: 13), nom. illeg. *Heliophila latisiliqua* E. Mey. ex Sonder (1846: 224) var. *latisiliqua* (Marais, 1966, 1970). Type, see above.

(b) **H. thunbergii** Steud. var. **macrostylis** (E. Mey. ex Sond.) B. Nord., comb. nov.
H. macrostylis E. Mey. ex Sonder (1846: 225). Type, see below.
H. latisiliqua E. Mey. ex Sond. var. *macrostylis* (E. Mey. ex Sond.) Marais (1966, 1970).

20. **Heliophila macrostylis** E. Mey. ex Sonder (1846: 225)

Type: Between Zilverfontein, Kooperbergen and Kaus, *Drège*, "*Helioph. macrostylis* EM." (S, lecto.!). Fig. 4A.

This now becomes a variety of *H. thunbergii* (see above), when Marais' opinion (1966, 1970) of its taxonomy is adopted. However, the two taxa may well deserve subspecific status, since they differ in a whole syndrome of morphological characters and are strictly allopatric. Var. *macrostylis* has a restricted distribution in northern Namaqualand, although it has been collected once in southernmost South West Africa (*Nordenstam 1167* in M, S). Var. *thunbergii* has a more southerly range in the western Cape Province, from Calvinia in the north to the Hex River Mountains in the south.

21. **Heliophila meyeri** Sonder (1846: 226)

Type: Caledon, Gnadenthal, *Drège*, "*Helioph. pectinata* Burch. a" (S, lecto.!). Sonder also cited a specimen in herb. E. Meyer.

Marais (1966, 1970) united this with *H. dentifera* Sond., which was published simultaneously (cf. No. 17 above), and chose the epithet *meyeri*.

22. **Heliophila crithmifolia** Willd. var. **laevis** Sonder (1846: 228)

Type: Between Zilverfontein, Kooperbergen and Kaus, *Drège*, "*Helioph. laevis* EM. a" (S, lecto.!). Sonder also saw a specimen in herb. E. Meyer.

Marais (1970) did not recognize any infraspecific taxa of the widespread and variable species *H. crithmifolia*.

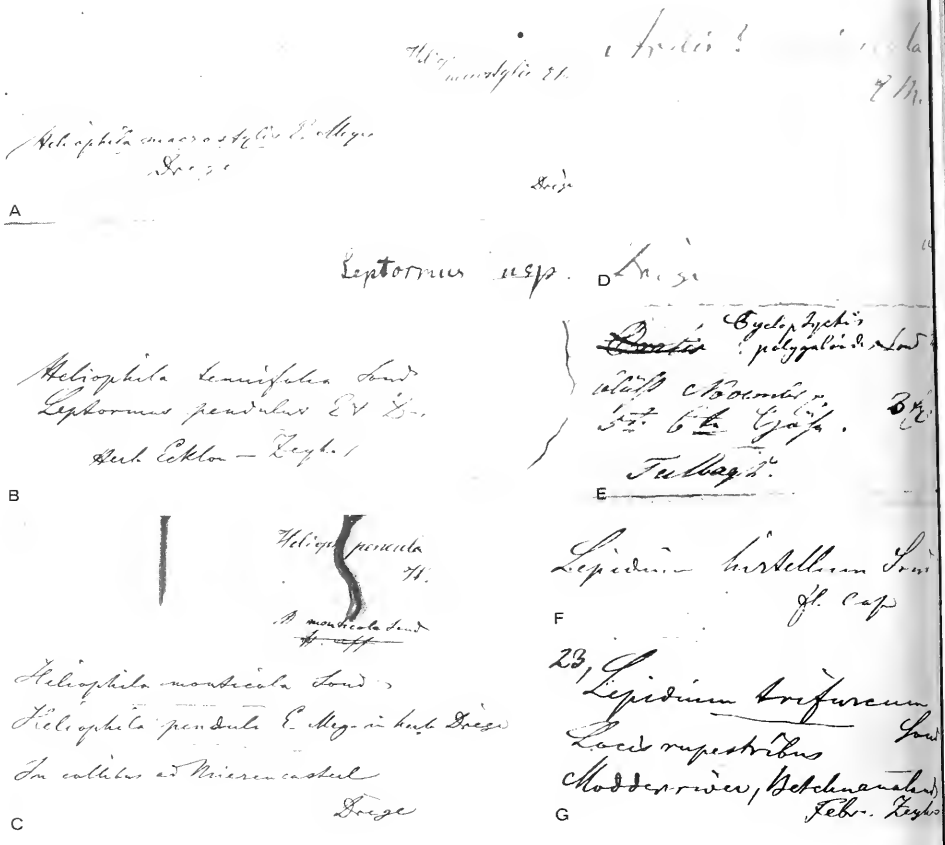


FIG. 4.
Labels of certain Sonder type specimens present in the Stockholm herbarium (S); A: *Heliophila macrostylis* E. Mey. ex Sond. The hand-writing seen in the upper right-hand corner is that of E. Meyer, otherwise Sonder's; B: *H. tenuifolia* Sond. Ecklon's hand-writing in upper right-hand corner, otherwise Sonder's; C: *H. monticola* Sond. Sonder's hand-writing, except for "*Helioph. pendula* W." which is that of E. Meyer; D: *Arabis nudiuscula* E. Mey. ex Sond. E. Meyer's hand-writing, except for "Drège" which was written by Sonder; E: *Cycloptychis polygaloides* Sond. The name was written by Sonder, the rest is Zeyher's hand-writing; F: *Lepidium hirtellum* Sond. Sonder's hand-writing; G: *L. trifurcum* Sond. Sonder's hand-writing.

23. **Heliophila viminalis** E. Mey. ex Sonder (1846: 231)

Type: Tulbagh, Nieuwekloof, *Drège*, "*Helioph. viminalis* EM." (S, lecto.!). Sonder also saw a specimen in herb. E. Meyer.

Marais' revision (1970) overlooked this species. It appears to be conspecific with *H. digitata* L. fil. (Marais, pers. comm., 1979) and should thus be added to the synonymy of the latter species.

24. **Heliophila tenuifolia** Sonder (1846: 232)

Type: Ecklon & Zeyher, sine loco, "*Leptormus pendulus* n sp" (in Ecklon's hand-writing, though otherwise annotated by Sonder, cf. Fig. 4B) (S, lecto.!).

This is one of four syntypes cited from herb. Berlin (B) and herb. Sonder. Now a synonym of *H. digitata* L. fil.

25. **Heliophila refracta** Sonder (1846: 234)

Type: Doornhoogde, Cape Flats, *Ecklon & Zeyher* (S, holo.!). Marais (1970) cited an isotype in SAM.

26. **Heliophila stricta** Sonder (1846: 236) nom. illeg., non Sims in Bot. Mag. t. 2526 (1825).

Syntypes: Bergvalley, *Ecklon & Zeyher*, "76.", leg. *Zeyher 1085* (S, lecto.! iso!); Riebekkasteel, *Drège 7549* (S!), *Drège 7571* (S!).

This now belongs to the widespread and variable species *H. africana* (L.) Marais. Incidentally, *H. glabra* (E. & Z.) Steud. should be added to the already extensive synonymy for that species given in Marais (1970).

27. **Heliophila pilosa** Lam. var. **debilis** Sonder (1846: 240)

Type: Zwarteberg, Caledon Baths, *Ecklon & Zeyher* (S, holo.!).

This is also one of the synonyms for *H. africana* (L.) Marais (1970).

28. **Heliophila cornuta** Sonder (1846: 246)

Type: Clanwilliam, Wupperthal, *Drège*, leg. *v. Wurmb*, "*Helioph. scoparia* Burch. c" (S, lecto.!).

This is the specimen illustrated by Sonder (1846, Plate 28), cf. Fig. 2C, D.

29. **Heliophila elata** Sonder (1846: 247)

Type: Clanwilliam, Ebenezar, *Drège 7566* "a" (S, lecto.!).

Marais (1970) cited an isotype in K.

30. **Heliophila rigidiuscula** Sonder (1846: 251)

Syntypes: Witte- and Zwartekeirivier (Tambukiland), at Windvogelberg and near Philippstown, *Ecklon & Zeyher* (S, lecto.!); between Kat- and Klipplaat-rivier (?), *Drège*, "*Helioph. suavissima* Burch.?" (S!); Omtendo, *Drège*, "*Helioph. subulata* Burch." (S!).

The lectotype chosen is both the best specimen and the one illustrated by Sonder (1846, Plate 27), cf. Fig. 2A, B.

31. **Heliophila dregeana** Sonder (1846: 260)

Type: Clanwilliam, Wupperthal, *Drège 6556* leg. *v. Wurmb* (S, holo.!).

A comparison between the type and Sonder's illustration (Fig. 3C, D) reveals that a few branches have at some time been detached from this specimen, possibly by Sonder himself before he despatched his South African herbarium to Stockholm (cf. Nordenstam, in press). Such removed fragments from the Sonder herbarium may now be represented in the herbaria at Melbourne (MEL) and perhaps also at Lyon (LY).

32. **Heliophila arenaria** Sonder (1846: 262)

Type: Clanwilliam, Ebenezar, *Drège 7568* (S, holo.!).

Marais (1970) saw an isotype at K.

33a. **Heliophila florulenta** Sonder (1846: 263)

Type: Uitenhage, Zwartkopsrivier, 1829, *Ecklon* (S, lecto.!), *Zeyher 1897* (S!).

The material distributed as Ecklon & Zeyher "101." probably consists of both these collections combined.

33b. **Heliophila florulenta** Sond. var. **obliqua** Sonder (1846: 263)

Type: Witpoortberg, *Drège*, "*Helioph. obliqua* EM." (S, lecto.!) Sonder probably also saw a specimen in herb. E. Meyer.

H. florulenta sensu stricto, as well as this variety, are now both synonyms for *H. brachycarpa* Meisn. (Marais, 1970).

ACKNOWLEDGEMENT

I wish to thank Mr W. Marais (Kew Herbarium) for giving me his opinion on the identity of *Heliophila viminalis* E. Mey. ex Sond.

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STRUCTURE OF THE MATURING TESTA OF *ACACIA GALPINII* BURTT DAVY

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Abstract

The epidermal cells of the testa undergo anticlinal elongation during development. The cell walls consist of cellulose and pectic substances, whilst lignin is absent. Just before maturity, callose is deposited on the anticlinal walls of the epidermal cells. Large intercellular spaces are formed between adjacent cells of the columnar subepidermal hour-glass cell layer. Tylose-like bodies are present in these intercellular spaces.

Uittreksel

STRUKTUUR VAN DIE TESTA VAN *ACACIA GALPINII* BURTT DAVY TYDENS RYPING

Gedurende ontwikkeling verleng die epidermale selle van die testa antiklinaal. Die wande bestaan uit sellulose en pektiese bestanddele, sonder lignien. Kort voor volwassenheid word kallose op die antiklinale wande van die epidermale selle neergelê. Groot intersellulêre ruimtes ontstaan tussen aangrensende kolomvormige selle van die subepidermale uurglas sellaag. Til-agtige liggame is in hierdie intersellulêre ruimtes teenwoordig.

1. Introduction

The testa of the Leguminosae seed has such a typical structure that fragments of material containing the external palisade-like epidermal cells and the underlying hour-glass cells may be recognized as belonging to this family (Corner, 1951). Seed structure within this family is, according to Corner, of fundamental importance in the classification of the members of the family, perhaps even to generic rank.

The structure of the seed of members of the genus *Acacia* may be used to differentiate between some of the subgenera and even some species (Watson, 1948; Vassal, 1963; Robbertse, 1973).

The work of Vassal (1975) has shown that relatively few differences exist between the structure of the testa of different *Acacia* species, although certain tendencies within this taxon may be elucidated by ratios calculated from cell size measurements.

The ontogeny of the testa appears to differ in detail only in different genera of the family. The work of Reeve (1946a, b) on *Pisum* and Sterling (1975) on *Phaseolus* reflects the basic similarities within the family.

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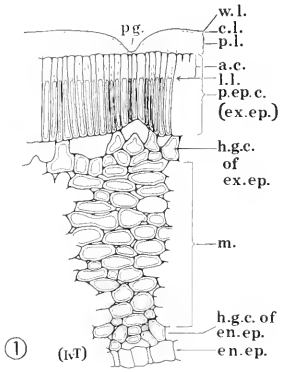


FIG. 1.

Diagram of a cross-section of a nearly mature testa. p.g.—pleurogram; w.l.—waxy layer; c.l.—cutinized layer; p.l.—pectic layer; a.c.—apical cap; l.l.—light line; p.ep.c.—palisade epidermal cells; ex.ep.—exo-epidermis; h.g.c.—hour-glass cells; m—mesophyll; en.ep.—endo-epidermis.

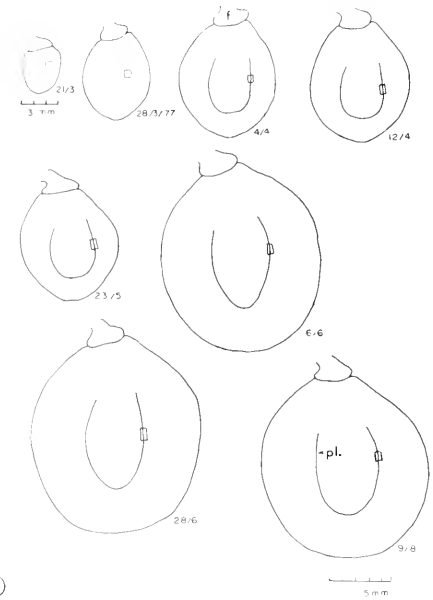


FIG. 2.

Size of seed at different ages and areas where testa was sampled. Dates when material was collected are indicated. pl.—pleurogram.

Acacia galpinii Burtt Davy was chosen for this study because the position of the light line in the testa does not vary appreciably in areas immediately adjacent to the pleurogram. The structure of these epidermal cells may therefore be regarded as being reasonably uniform for a considerable distance on both sides of the pleurogram. The structure and development of these cells are therefore less dependent on the exact area of the testa from which the studied material is obtained. A second reason is the slow development of the seeds, so that seed is available for study over an extended period.

The terminology used here is given in Figure 1 and is basically the same as that used by Corner (1951), with a few self-explanatory additions.

2. Material and Methods

All material was obtained from a stand of *Acacia galpinii* trees on the campus of the University of Pretoria. Flowers appear in August and the seeds reach a length of 1–2 mm in January of the following year. Fully mature seed is present in September or October.

Seeds were removed from pods, measured, and 1 mm wide strips of the testa, parallel to and including the pleurogram were cut out and placed in 6% glutaraldehyde in 0,05M Na-cacodylate buffer at pH 7,2. These strips were divided into lengths of 1,5 mm and fixed for a total period of 6 hours in the same solution. Post-fixation (2 h) was in 2% OsO_4 in the same buffer. Dehydration was done with ethanol or acetone with subsequent embedding in Spurr's (1969) medium. Figure 2 illustrates seeds at different ages as well as the position where samples of the testa were obtained.

Some duplicate batches of material were fixed and dehydrated at room temperature instead of 4 °C to compare the effect of temperature on the presence of microtubules, but no significant differences were found.

Thin (silver to gold) sections were cut with glass and diamond knives on a Reichert OMU 3 ultramicrotome. Sections were cut parallel to the long axes of the palisade epidermal cells, perpendicular to the pleurogram. Paradermal sections were cut from older material.

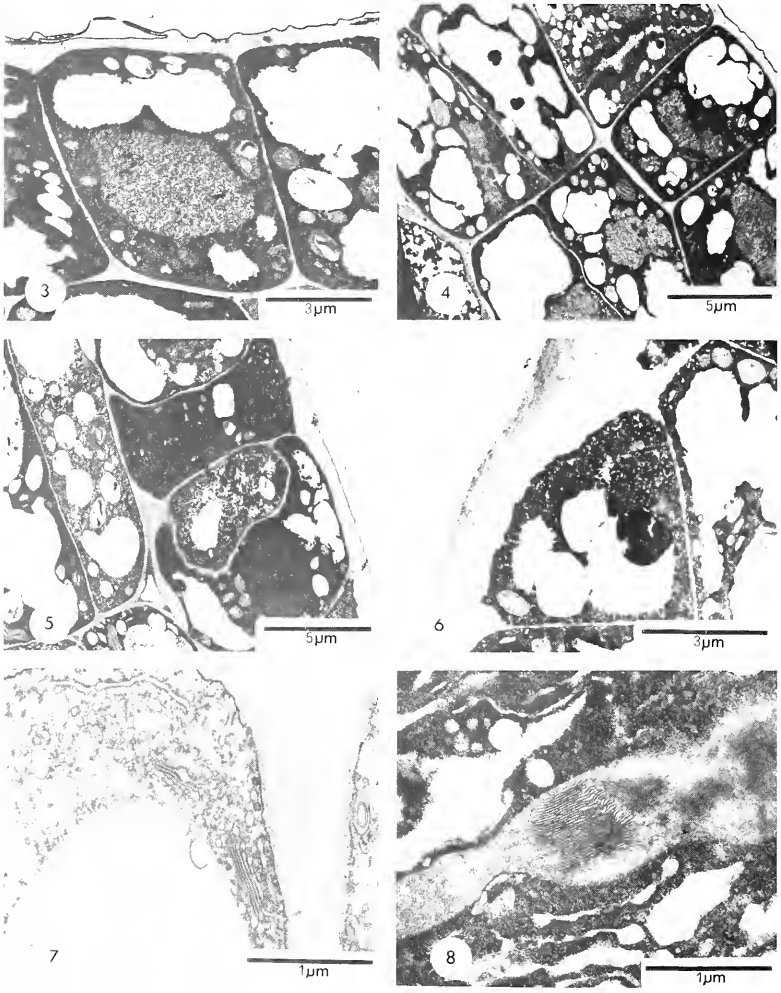
Contrast enhancement was either with potassium permanganate and lead citrate (Bray & Wagenaar, 1978) or with 4% uranyl acetate in 10% ethanol and lead citrate (Reynolds, 1963).

Sections (1–3 μm thick) of duplicate material fixed in buffered glutaraldehyde and embedded in glycol methacrylate (Feder & O'Brien, 1968) were cut with glass knives. These sections were stained with PAS-reagent (Nevalainen, Laitio & Lundgren, 1972) or with azure-methylene blue (Richardson, Jarret & Finke, 1960).

Histochemical tests were performed according to the standard procedures outlined by Jensen (1962). Some of the procedures used by Reeve (1946a) were

also applied. Representative sections were mounted in aniline blue (Smith & McCully, 1978) and examined with fluorescence optics.

Pieces of mature testa were mounted with epoxy adhesive on scanning electron microscope object carriers, broken or sectioned and sputter coated with 100 nm of gold. Fixation and critical point drying was found to be superfluous in the examination of the thick-walled epidermal cells at low magnification.



3. Results and Discussion

The exo-epidermal cells of very young seeds (less than 3 mm long) have the general form of parenchyma cells although their outer walls may already be slightly thickened. Nuclei are situated centrally and large vacuoles are present near the inner and outer tangential walls of the cells. Small vacuoles are abundant and seem to be formed from centres very near to each other and to the large vacuoles because they often cause indentations of the membranes of adjacent vacuoles (Figs 3 & 4). This indentation may also be due to the fusion of small vacuoles to form fewer, large vacuoles. The cuticle is very thin and parts may flake off. The inner tangential walls begin to thicken at approximately this stage of development, while the radial walls remain thin until later. Due to convolutions of the radial walls, as well as to anticlinal divisions, the cells may assume unusual shapes (Figs 5 & 6). The outer cutinized part of the cell wall is laid down in layers parallel to the external surface.

When the seed is nearly 5 mm long, the exo-epidermal cells start to elongate. This elongation process continues until the seed is nearly mature and the typical palisade-like shape is reached. The formation of a system of longitudinal cell wall grooves and ridges is initiated at about the time when radial elongation of these cells commences. These grooves and ridges are responsible for the characteristic shape of the mature epidermal cells (Fig. 16).

Pectic substances which are added to the developing outer walls appear to shrink after deposition, with the result that the middle lamella (or regions corresponding to the position of the original middle lamella) assumes the shape of a wrinkled line. A few cells exhibit coarse lamellae of pectic materials alternating

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Fig. 3.
Flaking cuticle on slightly thickened outer cell wall of 2 mm seed.

Fig. 4.
Vacuoles with indented membranes (arrowed) in exo-epidermal cells. Subepidermal cells exhibit newly formed periclinal cell walls. Seed 2,5 mm long.

Fig. 5.
Cell arrangement resulting from oblique anticlinal divisions. Seed 2,5 mm long.

Fig. 6.
Prismatic epidermal cell with distinct layering of wall material. Seed 3 mm long.

Fig. 7.
Apical part of exo-epidermal cell with dictyosomes and vesicles as well as rough endoplasmic reticulum orientated parallel to the developing cell wall. Seed 11 mm long.

Fig. 8.
Large, apparently inactive dictyosome in the basal part of an exo-epidermal cell from a 11 mm seed.

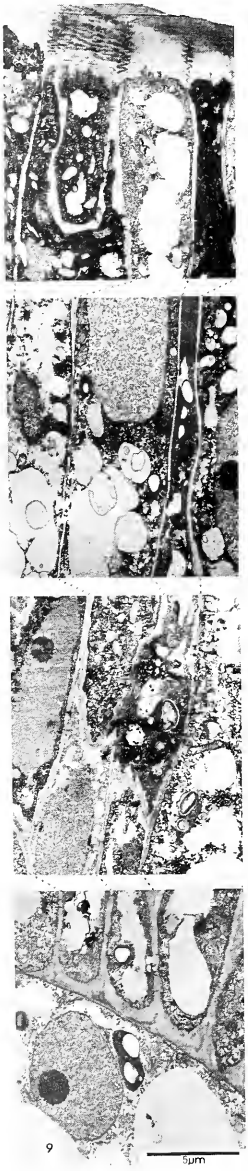


FIG. 9.
Composite electron micrograph of palisade epidermal cells from a 11 mm seed.

with presumably non-pectic subtances (Fig. 9). Most cells, however, do not show these coarse, alternating layers and appear finely fibrillar, with fibrils arranged parallel to the outer surface.

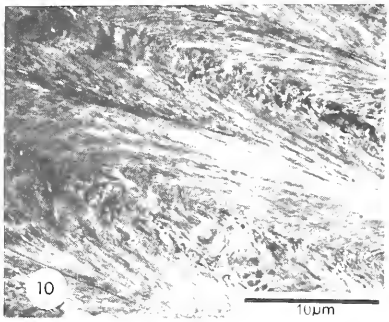
Large concentrations of sheets of rough endoplasmic reticulum are visible when the seed is approximately 11 mm long. These sheets are mostly arranged parallel to the developing walls. Whether this arrangement is of great importance, as Sterling (1975) implies, or whether it is a function of the fact that the cells are highly vacuolate with a thin layer of cytoplasma appressed to the cell walls, is not clear. Aggregations of polyribosomes and dictyosome cisternae with coated and uncoated vesicles are conspicuous near all developing cell walls, but are especially prominent near the apical ends of the exo-epidermal cells (Fig. 7). Many of these vesicles appear to coalesce with the plasmalemma. Dictyosomes consisting of approximately 30 closely appressed cisternae are occasionally present in the central or basal parts of these cells (Fig. 8). These dictyosomes do not appear to be active in secretion of vesicles, and the two faces of the complex are not nearly as well differentiated as that of the smaller, apically situated dictyosomes. These large dictyosomes are usually found close to the radial compartmenting walls.

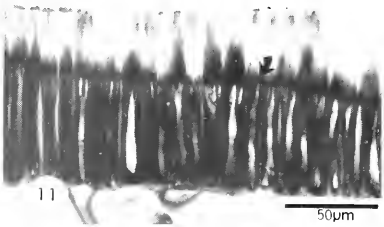
Very few microtubules are visible at any stage in the development of the epidermal cells, as was also found by Sterling (1975) during his study of the formation of secondary cell walls of integuments in *Phaseolus*. Lipid bodies with multi-layered envelopes are present near the cell wall in most epidermal and mesophyll cells.

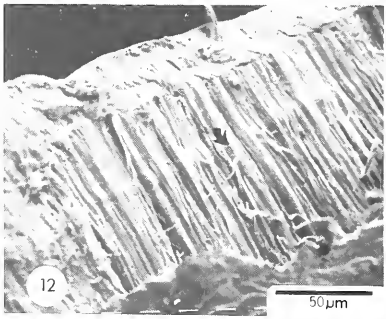
When the seeds reach a length of approximately 15 mm, size is no longer a reliable indication of maturity. Relatively large seeds may be less developed, when judging maturity by the thickness of epidermal and hour-glass cell walls, than appreciably smaller seeds.

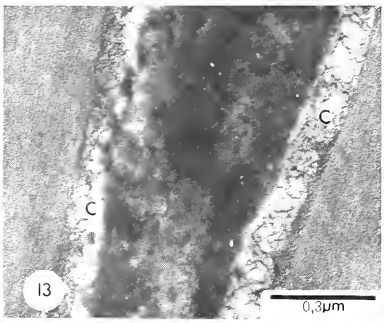
When seeds are still less than 15 mm in length, the outer walls of the exo-epidermal cells have already undergone a great deal of thickening and (compare Fig. 1) consist of a thin, superficial waxy layer, a cutinized layer 3–5 μm thick, a pectic layer of nearly 10 μm and apical caps which may be 20 μm wide. The luminate basal parts of the cells may be a further 20 μm long. Ultimately, in fully mature seeds, the total length of the epidermal cells may be as much as 150 μm in the areas not directly associated with the pleurogram. This size is reached through continual increase in the thickness of all layers, except possibly the outermost cutinized layer. The cell wall material laid down in the apical caps is coarsely lamellar and is initially deposited nearly parallel to the middle lamella. Lamellae deposited at a slightly later stage are laid down in progressively more acute conical formations. The youngest parts of these cell walls which are deposited later and which occlude the lumina of the apical parts of the cells are apparently randomly arranged and not completely solid (Fig. 10) due to inclusions of probably cytoplasmic origin. According to Sterling (1975) the epidermal cell walls consist of nearly pure, highly crystalline cellulose in fibrous crystallites.

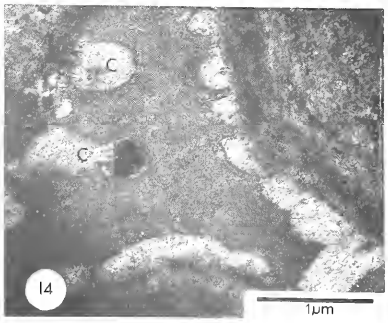
Histochemical tests, however, confirm the findings of Reeve (1946a) on the testa of *Pisum*, in that the apical ends of the cells test positive for pentosans. In this area of the wall, anticlinally orientated irregularities are present, which may be the same as the microchannels observed by Lyshede (1978) in the outer epidermal walls of stems of *Spartocytisus* of the Fabaceae. The irregularities observed here in the arrangement of the lamellar wall thickenings, are, however, not as clear as

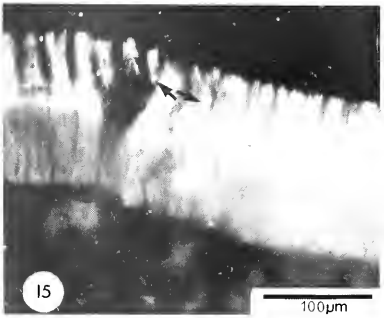












those found by Lyshede and are visible only in electron micrographs. Typical microchannels should also be visible with the optical microscope, as implied by Hülsbruch (1966). These channels may be the route by which pectins and hemicellulose are deposited in the apical parts of the cell wall. The basal parts of the cells contain less of these substances. No lignin could be demonstrated by means of any of the usual tests in any cells of the testa, except in the vascular tissue. Cell wall material in these basal parts of the cells stain very deeply with the P.A.S.-procedure (Fig. 11) with the light line included in this darkly staining area. The position of the light line in this part of the testa is approximately in the middle or the upper third of the epidermal cells, as was also observed by Vassal (1975). When mature integuments are fractured and examined in the scanning electron microscope, the light line appears to be located at the position of a definite structural entity, consisting of a localized broadening of the cell wall (Fig. 12). This increase in width of the cells may be due to the measure of elasticity supplied to the cell walls by the presence of the flutes in the wall (Fig. 16). This may give rise to the refraction of light which is usually accepted to be the cause of this phenomenon, rather than the presence of a structural feature (Lute, 1928; Hamly, 1935; Corner, 1951).

Just before full maturity of the seeds is attained, large amounts of callose-like material are deposited onto (Fig. 13) and into (Fig. 14) the cell wall. This can also be seen when the cells are lightly stained with dilute aniline blue at physiological pH values and examined with fluorescence optics (Fig. 15). This appears to be in agreement with the findings of Reeve (1946a) who showed the presence of

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FIG. 10.
Coarsely lamellar nature of cell wall thickenings initially laid down approximately parallel to the middle lamella and later assuming the characteristic conical shape. Seed 11 mm long.

FIG. 11.
P.A.S.-stained section of testa from 11 mm seed, showing the position of the light line (arrowed).

FIG. 12.
Fractured mature testa, illustrating the localized broadening of the cell walls at the position of the light line (arrowed).

FIG. 13.
Callose-like material (C), deposited on the cell wall of nearly mature exo-epidermal cells as seen in longitudinal section.

FIG. 14.
Callose-like material (C) deposited in the wall of exo-epidermal cells of a nearly fully mature testa. Paradermal section.

FIG. 15.
Fluorescence of callose (arrowed) in the apical parts of mature exo-epidermal cells.

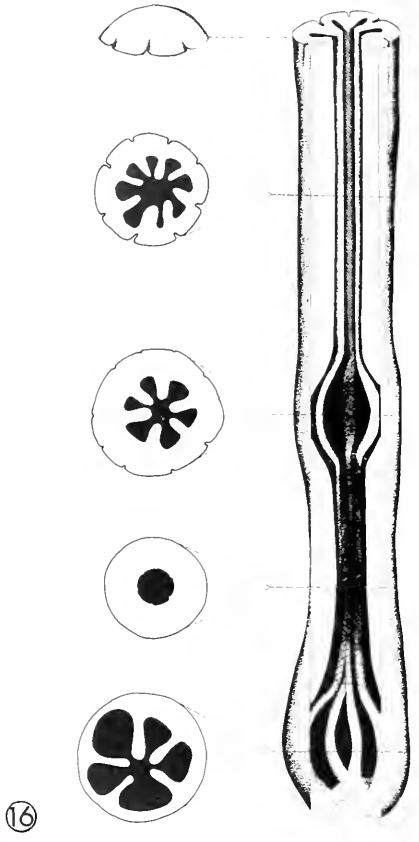


FIG. 16.
The structure of a mature epidermal cell, excluding all layers external to the apical cap.

"encrusting pentosan materials", especially in the light line area and in the middle lamellae of fully mature integuments of *Pisum*.

Tannin deposits are present in nearly all mature cells of the testa. The time of initiation of such deposits is, however, very variable. Some seeds contain appreciable amounts of tannin when the seed is less than 4 mm long. In other cases, seeds as large as 14 mm show little evidence of such deposition. Tannin is, however, nearly always present in exo-epidermal cells of seeds longer than 5 mm.

Up to the time when the cells of the exo-epidermis start to elongate, the development of the endo-epidermal cells proceeds along very similar lines. At later stages of development, the endo-epidermal cells increase in width by means of cell enlargement. Anticlinal divisions occur in a few of the cells. The endo-epidermal cells initially remain thin walled and never elongate periclinally to form palisade-like cells such as the exo-epidermis. At about the 11 mm seed size, some radial walls of these cells appear to be perforate (Fig. 17). Whether this is due to localized lysis of the cell wall, or to the ingrowth of the walls, is not clear. Due to the pressure of the developing cotyledons, the anticlinal walls are folded. These folds are supplemented by localized growth of these anticlinal walls (Figs 18 & 19).

At maturity the first subepidermal cell layer below each epidermis shows the typical columnar structure as well as large intercellular spaces. These cells are basally and apically wider than in the centre, so that the term hour-glass cell, is very appropriate. A survey of the literature shows that both the terms "hour-glass cells" and "osteosclereids" are freely applied to these cells. With regard to the complete absence of lignin from the walls of these cells and the characteristic shape, peculiar to the testa of the Leguminosae, the name hour-glass cells should perhaps be given preference.

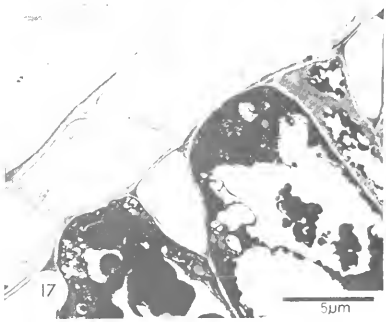
The hour-glass cells are initially thin walled and divide periclinally (Fig. 20). Anticlinal divisions occur very seldom except in the area immediately below the pleurogram. It appears as if this subepidermal hour-glass cell layer keeps pace with the increase in seed size by means of lateral stretching. This leads to tension in this layer, which can, in this case, only be relieved by the formation of large intercellular spaces. These spaces start to appear when the seed is ca. 5 mm long. The development of the hour-glass cells of the endo-epidermis proceeds along similar lines to those of the exo-epidermis, but these cells are not as extremely adapted.

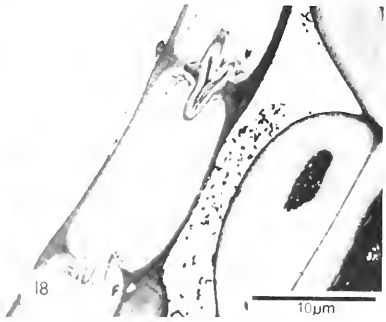
This degree of development of the hour-glass cell layers is typical of the subgenus *Aculeiferum* (Vassal, 1975) or, according to Robbertse (1973), the subgenus *Vulgares*.

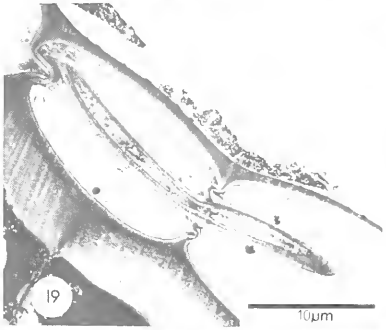
The development of the hour-glass cells is essentially complete when the seeds are about 20 mm long but still not mature. Intercellular deposits of tannin may be present (Fig. 18) in the cavities adjoining the epidermal cells.

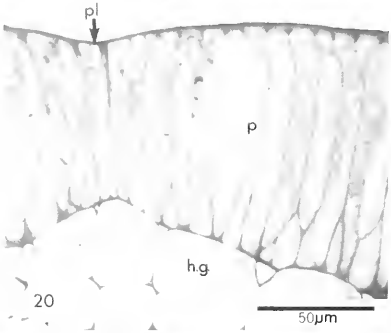
Tylose-like bodies appear to be extruded from the basal parts of the exo-

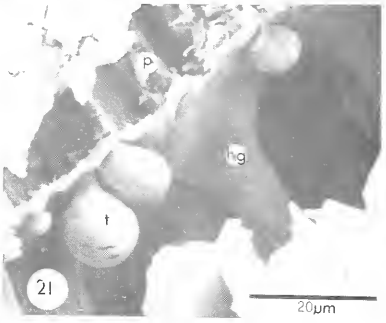
epidermal cells and are present in the intercellular spaces between the epidermal and hour-glass cells (Figs 21 & 22). These bodies contain significantly more silicon than adjacent cells (as monitored by microprobe X-ray analysis). If the epidermal cell contents are under pressure, while a low pressure area exists in the intercellular spaces of the hour-glass cells, such tylose-like extrusions could be formed when thin areas of the basal cell walls of exo-epidermal cells bulge outwards.

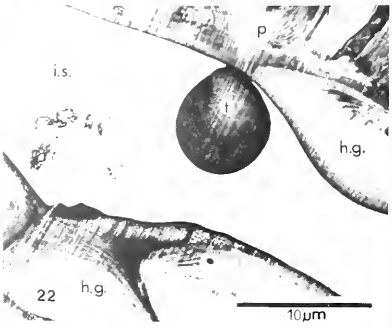












None of the sections examined, however, showed continuity between the cytoplasm of the epidermal cells and presumed cytoplasmic inclusions of the tylose-like bodies.

The pleurogram is visible in immature seeds as a localized area where the exo-epidermal cells are shorter than the cells from other areas (Fig. 20). The area at the base of these shorter cells are filled in by cells formed by periclinal divisions in the young subepidermal hour-glass cells. In mature seeds the groove thus formed is made more prominent by the deposition of the pectic layer in areas lateral to the pleurogram.

ACKNOWLEDGEMENTS

Miss I. von Teichmann und Logischen provided valuable technical assistance. This work was supported by a grant of the South African C.S.I.R. to the first author.

Thanks are due to the head and staff of the Department of Botany, University of Pretoria for making all facilities available.

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FIG. 17.
Perforate radial walls of endo-epidermis in a 11 mm seed.

FIG. 18.
Folded anticlinal walls of the endo-epidermis, with tannin in the intercellular spaces between hour-glass cells.

FIG. 19.
Result of pressure and growth on the anticlinal walls of endo-epidermal cells from a 19 mm seed.

FIG. 20.
Thin walled hour-glass cells (h.g.) and palisade epidermal cells (p) of a 8 mm seed, sectioned through the pleurogram (pl).

FIG. 21.
SEM microcraph showing tylose-like bodies (t), hour-glass cells (h.g.) and palisade epidermal cells (p) in a mature seed.

FIG. 22.
Electron micrograph of a section through a tylose-like body of a 20 mm seed. i.s.—intercellular space; t—tylose-like body; h.g.—hour-glass cell; p—palisade epidermal cell.

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Jl S. Afr. Bot. 46 (3): 279–281 (1980)

APPLICATION OF THE NAME *PELARGONIUM TABULARE* (GERANIACEAE)

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ABSTRACT

1. The name *Pelargonium tabulare* (Burm. f.) L'Hérit. (1789) which is based on *Geranium tabulare* Burm. f. (1759), is the correct name for the species hitherto known as *P. saniculaefolium Willd.* (1800). 2. *P. elongatum* (Cav.) Salisb. is the correct name for the species which has hitherto erroneously been known as *P. tabulare.*

UITTREKSEL

DIE GEBRUIK VAN DIE NAAM *PELARGONIUM TABULARE* (GERANIACEAE)

1. Die naam *Pelargonium tabulare* (Burm. f.) L'Hérit. (1789) wat baseer is op *Geranium tabulare* Burm. f. (1759), is die regte naam vir die spesie wat tot dusver bekend was as *P. saniculaefolium Willd.* (1800). 2. *P. elongatum* (Cav.) Salisb. is die regte naam vir die spesie wat tot dusver verkeerdelik bekend was as *P. tabulare.*

Geranium tabulare was first described by Burman (1759), whose description refers to a plant with a long-petioled, glabrous leaf. A specimen named by Burman is still being preserved in G (see below), and agrees well with a species known to have coriaceous, glabrous and somewhat glaucous leaves.

The name *G. tabulare* was taken up by Linnaeus (1763). Although he cited Burman (1759), his description "folia . . . nuda, ad marginem hirta" refers to another species. This is confirmed by a specimen (sheet no. 858.18 in LINN!) bearing the inscription "Geranium tabulare" in what is thought to be Linnaeus' handwriting. This sheet matches a species known to have slightly scabrous leaves with glandular hairs which are especially noticeable on the leaf margins.

The name was again taken up and used in its original context by Cavanilles (1787). In addition Cavanilles described a new species, *G. elongatum*, which is conspecific with LINN 858.18.

In 1789 L'Héritier transferred *Geranium tabulare* to the genus *Pelargonium*, but in doing so created a confusion about the identity of *P. tabulare* which has persisted up to the present. Firstly, L'Héritier did not cite Burman's original publication (1759). He did cite Linnaeus (1763) which may or may not be interpreted as citing Burman by implication. Secondly, it appears as if L'Héritier's concept is heterogenous:

1. (a) His description includes the phrase "caulibus decumbentibus pilosus" which is reminescent of *P. alchemilloides* (L.) L'Hérit.
1. (b) He referred to his own *Geraniologia* t. 9 (1792). This illustration depicts hairy petioles, unlike Burman's plant. The leaves are not depicted well enough

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for positive identification, but the stipules are broadly triangular, and together with the hairy petioles seem to indicate *P. alchemilloides* as well.

2. He cited *Geranium elongatum* Cav. (1787).

It is therefore not possible to define L'Héritier's concept of *P. tabulare* with certainty, but it is clearly different from *Geranium tabulare* Burm. f. However, Article 55 of the *International Code of Botanical Nomenclature* (1978 edition) states ". . . When, on transference to another genus, the specific epithet has been applied erroneously in its new position to a different species, the new combination must be retained for the species to which the epithet was originally applied, and must be attributed to the author who first published it". The fact that L'Héritier and subsequent authors applied the name *Pelargonium tabulare* to a species other than *Geranium tabulare* Burm. f. is therefore of no nomenclatural consequence. Accordingly Harvey's (1860) and Knuth's (1912) application of the name *Pelargonium saniculaefolium* Willd. for *Geranium tabulare* is erroneous and this name should be regarded as a synonym rather than the correct name of *G. tabulare*. The correct citation for Burman's species is therefore as follows:

Pelargonium tabulare (Burm. f.) L'Hérit. in Ait., Hort. Kew, ed. 1, **2:** 419 (1789), non *P. tabulare* sensu auct. mult.

Geranium tabulare Burm. f., Ger.: 36, t. 1, f. 44 (1759); Cav., Diss. **4:** 232, t. 100, f. 2 (1787); Thunb., Prodr. **1:** 113 (1794); non L., Sp. Pl. ed. 2, **2:** 947 (1763) Type: CAPE—"*Cap.* BON SPEI montibus", *Burman coll. 46* (G, holo.!).

Pelargonium saniculaefolium Willd., Sp. Pl. **3:** 673 (1800); Pers., Syn. Pl. **2:** 229 (1807); DC., Prodr. **1:** 668 (1824); Spreng., Syst. Veg. **3:** 61 (1826); Harv. in Fl. Cap. **1:** 294 (1860); Knuth in Pflanzenr. **4**, 129: 426 (1912); Adamson & Salter, Fl. Cape Penins.: 517 (1950); Kidd, Wild Flow. Cape Penins.: t. 85 (1950). Type: CAPE—"Cap. b. spei" (B. holo.!).

In publications subsequent to L'Héritier (1789), the name *P. tabulare* has been applied to a species conspecific with LINN 858.18, characterized by long and somewhat hairy petioles, laminae which may appear glabrous at a first glance but which actually are hirsute with glandular and non-glandular hairs (this is most noticable at the leaf margins), and lanceolate or narrowly triangular stipules, by authors including Willd., Sp. Pl. **3:** 656 (1800); Pers., Syn. Pl. **2:** 229 (1807); Ait. f., Hort. Kew. ed. 2, **4:** 167 (1812); DC., Prodr. **1:** 660 (1824); Harv. in Fl. Cap. **1:** 296 (1860); Knuth in Pflanzenr. **4**, 129: 431 (1912); Adamson & Salter, Fl. Cape Penins.: 517 (1950); Kidd, Wild Flow. Cape Penins.: t. 70 (1950) and J. J. A. v. d. Walt, Pelargoniums S. Afr.: 44 (1977).

However, this application of the name *Pelargonium tabulare* is erroneous, and the correct citation for this species should be:

Pelargonium elongatum *(Cav.) Salisb.*, Prodr. 312 (1796); Steud., Nom. Bot. ed. 2, **2:** 285 (1841).

Geranium elongatum Cav., Diss. **4:** 233, t. 101, f. 3 (1787); Thunb., Prodr. **1:** 113 (1794). Type: CAPE—"ad Caput Bonae Spei" (MA, holo!).
P. tabulare auct. mult., non *Geranium tabulare* Burm. f. (1759).

ACKNOWLEDGEMENTS

The authors wish to record their appreciation to Dr D. J. B. Killick of the Botanical Research Institute in Pretoria for commenting on the manuscript.

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Jl S. Afr. Bot. 46 (3): 283–292 (1980)

NAME CHANGES IN *PELARGONIUM* (GERANIACEAE)

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ABSTRACT

1. The new name *Pelargonium magenteum* J. J. A. v. d. Walt is designated for *P. rhodanthum* Schltr. (1900), non Sweet (1825). 2. The new name *P. sericifolium* J. J. A. v. d. Walt is chosen for *P. sericeum* E. Mey. ex Harv. (1860), non Salisb. (1796). 3. The name *P. auritum* (L.) Willd., based on *Geranium auritum* L. (1753), is the correct name for *P. hirsutum* (Burm. f.) Ait. (1789) which is based on *Geranium hirsutum* Burm. f. (1759). *P. hirsutum* var. *melananthum* (Jacq.) Harv. is synonymous with *P. auritum* subsp. *auritum*. The new combination *P. auritum* subsp. *carneum* (Harv.) J. J. A. v. d. Walt is made from *P. hirsutum* var. *carneum* Harv. 4. The name *P. oreophilum* Schltr. is re-instated, as it is shown to have been erroneously placed in the synonymy of *P. hirtum* (Burm. f.) Jacq. 5. *P. populifolium* Eckl. & Zeyh. is placed in the synonymy of *P. ribifolium* Jacq. A specimen in Vienna (W) should be considered the holotype of *P. ribifolium*. 6. The name *P. abrotanifolium* (L.f.) Jacq. is applied to a highly variable group of specimens. Material previously designated *P. incisum* (Andr.) Willd. is included under *P. abrotanifolium*, but the application of the name *P. incisum* is problematical.

UITTREKSEL

NAAMSVERANDERINGE IN *PELARGONIUM* (GERANIACEAE)

1. Die nuwe naam *Pelargonium magenteum* J. J. A. v. d. Walt word gegee aan *P. rhodanthum* Schltr. (1900), non Sweet (1825). 2. Die nuwe naam *P. sericifolium* J. J. A. v. d. Walt word gekies vir *P. sericeum* E. Mey. ex Harv. (1860), non Salisb. (1796). 3. Die naam *P. auritum* (L.) Willd. wat baseer is op *Geranium auritum* L. (1753), is die regte naam vir *P. hirsutum* (Burm. f.) Ait. wat baseer is op *Geranium hirsutum* Burm. f. (1759). *P. hirsutum* var. *melananthum* (Jacq.) Harv. is sinoniem met *P. auritum* subsp. *auritum*. Die nuwe kombinasie *P. auritum* subsp. *carneum* (Harv.) J. J. A. v. d. Walt word gemaak van *P. hirsutum* var. *carneum* Harv. 4. Die naam *P. oreophilum* Schltr. word weer in gebruik geneem, omdat dit gevind is dat dit verkeerdelik beskou is as 'n sinoniem van *P. hirtum* (Burm. f.) Jacq. 5. *P. populifolium* Eckl. & Zeyh. word geplaas in die sinonomie van *P. ribifolium* Jacq. Daar is 'n eksemplaar in Wenen (W) wat as die holotipe van *P. ribifolium* beskou behoort te word. 6. Die naam *P. abrotanifolium* (L.f.) Jacq. word toegepas op 'n hoogs variërende groep eksemplare. Materiaal wat voorheen benaam is as *P. incisum* (Andr.) Willd. word ingesluit onder *P. abrotanifolium*, maar die toepassing van die naam *P. incisum* is problematies.

NEW NAME FOR *P. RHODANTHUM* SCHLTR.

The name *Pelargonium rhodanthum* was first used in 1825 by Sweet for a horticultural hybrid of unknown parentage. It is not known whether this hybrid has survived in cultivation.

In 1900 Schlechter used the same name when describing a new species from near Clanwilliam. As the name had previously been used in another context,

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P. rhodanthum Schltr. is a later homonym of *P. rhodanthum* Sweet and has to be discarded. No name later than 1900 is available for Schlechter's species, and, surprising as it may seem for such a conspicuous and relatively widespread species which occurs in an area long traversed by numerous plant collectors, no earlier name seems to be available either. We therefore designate the following new name:

Pelargonium magenteum J. J. A. v. d. Walt, nom. nov.

P. rhodanthum Schltr. in Bot. Jb. **27:** 152 (1900); Knuth in Pflanzenr. **4,** 129: 451 (1912); J. J. A. v. d. Walt, Pelargoniums S. Afr.: 41 (1977); non *P. rhodanthum* Sweet, Geran. **3:** 282 (1825).

Type: CAPE—"In arenosis montis Packhuisberg, in ditione Clanwilliam", *Schlechter 8662* (B^+, holo.; Z, lecto.!; BM!; BOL!; E!; G-DC!; GRA!; K!; L!; P, 2 sheets!; S!; W!).

New Name for *P. sericeum* E. Mey. ex Harv.

The name *Pelargonium sericeum* was first used in 1796 by Salisbury (Prodr.: 315) for a species previously known as *P. crassicaule* L'Hérit., Geran.: t. 26 (1792). It is not clear why Salisbury gave the new name, as there seems to have been no need to replace L'Héritier's name. As such, Salisbury's name has no nomenclatural standing, being a superfluous name. The name *P. sericeum* was again applied by E. Meyer [Drège, Zwei Pfl. Doc.: 209 (1843)] for another species, but without furnishing a description. This name was subsequently validated when published together with a description by Harvey [in Fl. Cap. **1:** 282 (1860)]. As *P. sericeum* E. Mey. ex Harv. is a later homonym of *P. sericeum* Salisb., it is illegitimate. As no alternative name is available for *P. sericeum* E. Mey, ex Harv., we choose the following new name for this species:

Pelargonium sericifolium J. J. A. v. d. Walt, nom. nov.

P. sericeum E. Mey. in Drège, Zwei Pfl. Doc.: 209 (1843), nom. nud.; ex Harv. in Fl. Cap. **1:** 282 (1860); non Salisb. (1796).

Type: CAPE—Kaus Mountain, near Goedman's Kraal, *Drège s.n.* (? TCD, holo., not seen; G, 3 sheets!; ? K, not seen; L!; ? MEL, not seen; OXF!; P, 3 sheets!; PRE!; S!; SAM!).

The name *Pelargonium setosum* which appears on some herbarium sheets is a manuscript name without any nomenclatural standing.

Correct Name for *P. hirsutum* (Burm. f.) Ait.

It has become evident that the name *Pelargonium hirsutum* (Burm. f.) Ait.

(1789), based on *Geranium hirsutum* Burm. f. (1759), is preceded by the name *P. auritum* (L.) Willd. (1800) which is based on *Geranium auritum* L. (1753) and refers to the same species.

Harvey in Fl. Cap. **1:** 267 (1860) enumerated two varieties of *P. hirsutum*, viz. var. *melananthum* (Jacq.) Harv. which is based on *P. melananthon* Jacq. (1791), and var. *carneum* Harv.

We have no doubt that both these varieties represent a single species, characterised by dense golden-yellow hirsute hairs on the lamina, the petiole and even on the peduncle. There is a considerable variation in the shape of the lanceolate lamina, from entire to deeply pinnatifid and even bi-pinnatifid or almost pinnatipartite. This variation does however not have any taxonomic significance, as it cannot be correlated with any other characteristics and a single plant may exhibit several or all these variations.

In our opinion the correlation between morphological differences and geographical distribution does however indicate a subspecific relationship between the two variants. It is true that according to the available information there is a slight overlap in the distribution areas of the two subspecies which may indicate that a certain amount of gene-flow takes place between them in the area of mutual contact. Field studies in this area should yield valuable information on the reproductive behaviour of the two subspecies. Occasional records of light-flowered individuals within the distribution area of the dark-flowered subspecies or vice versa are not above suspicion, and will have to be verified in the field.

The correct citation is as follows:

Pelargonium auritum (L.) Willd., Sp. Pl. **3:** 644 (1800).

subsp. **auritum**

Geranium auritum L., Sp. Pl. ed. 1, **2:** 679 (1753). Iconotype: "Comm. hort. 2. p. 121" (unpublished plate in Moninckx collection in Amsterdam!).
Geranium hirsutum Burm. f., Spec. Geran.: 50, t. 2, f. 68 (1759). Type: CAPE—"Cap. BON. SPEI" (G, lecto.!).*
Pelargonium hirsutum (Burm. f.) Ait., Hort. Kew. ed. 1, **2:** 417 (1789); Knuth in Pflanzenr. **4,** 129: 339 (1912).
P. melananthon Jacq., Coll. **4:** 188 (1791). Type: "Ex Promontorio bonae Spei" (W, holo.!).
P. hirsutum (Burm. f.) Ait. var. *melananthum* (Jacq.) Harv. in Fl. Cap. **1:** 267 (1860); Knuth op. cit. p. 340; J. J. A. v. d. Walt, Pelargoniums S. Afr.: 21 (1977).

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* This specimen was chosen and labelled as lectotype because of the three specimens of this species in the Burman collection, it bears the closest resemblance to the illustration which accompanied the original description.

subsp. **carneum** (Harv.) J. J. A. v. d. Walt, comb. & stat. nov.

P. hirsutum (Burm. f.) Ait. var. *carneum* Harv. in Fl. Cap. **1:** 267 (1860); Knuth op. cit. p. 340; non *P. carneum* Jacq. (1791). Syntypes: CAPE—without precise locality, *Ecklon & Zeyher 468* (S!); *482* (S!), *483, 484, 485* (S!), *494; Drège 7490b* (S!), *7491* (CGE!; K!;S!), *7493*.

For a more complete synonymy we refer to Knuth (l.c.). For the subsp. *carneum* various older epithets are available, but as none of these are in subspecific or varietal rank, they do not have priority over the epithet *carneum* (Article 11 of the 1978 edition of the *International Code of Botanical Nomenclature*). The epithet *carneum* is here retained in preference to an earlier epithet in the interest of nomenclatural stability.

TABLE 1.
Pelargonium auritum: comparison of the two subspecies.

	subsp. *auritum*	subsp. *carneum*
Geographical distribution	South Western Cape, mainly west of E 22°	Southern Cape, mainly east of E 22°
Colour of petals	Dark purple black	White to light pink with red to purplish veins
Average dimensions of petals (mm): 2 posterior	11 × 2,5	13 × 2,5
3 anterior	9 × 1,5	10 × 1,5
Margins of petals	Conspicuously undulate	Slightly undulate to plane

RE-INSTATEMENT OF THE NAME *P. OREOPHILUM* SCHLTR.

Pelargonium oreophilum Schltr., based on *Schlechter 8650* (BOL!; E!; PRE, 2 sheets!; Z!) was described from "Packhuis-Berg" near Clanwilliam in Bot. Jb. **27:** 151 (1900). Knuth in Pflanzenr. **4,** 129: 381 (1912) reduced it to a synonym under *P. hirtum* (Burm. f.) Jacq., where its position remained unquestioned up to the present time.

Under Knuth's concept of *P. hirtum*, two distinct populations can be distinguished, which differ from each other in a number of morphological characteristics. The first of these populations, to which Burman's name *Geranium hirtum* was originally applied, occurs on the Atlantic coastal plain between Cape Town and St. Helena Bay, while the population to which the name *P. oreophilum* applies, occurs to the north-east of the former population in a relatively restricted area in the Cedarberg range. The plants of the two populations exhibit a strong mutual resemblance on account of the hirsute, 1–2 pinnatifid-pinnate leaves. The

most conspicuous differences between the two populations are in the mode of attachment of the stipules, and in the petals. In *P. oreophilum* the stipules are attached to the petiole at their very bases only, while in *P. hirtum* they are adnate to the petiole for at least ½ their total length. In *P. oreophilum* the petals are narrowly obovate without claws and the two posterior petals are sharply and strongly reflexed, while in *P. hirtum* the petals are broadly obovate with conspicuous claws and the two posterior petals are not reflexed. (Fig. 1). In both populations the petals occur in various shades of pink. The differences between the two populations can be correlated with several more characteristics, as shown in Table 2.

It is concluded that the number and magnitude of the differences between the two populations warrant specific distinction, and accordingly we re-instate the name *P. oreophilum* Schltr. for the population in the Cedarberg.

TABLE 2.
Comparison of *Pelargonium oreophilum* and *P. hirtum* (average dimensions in brackets).

Characteristic	*P. oreophilum*	*P. hirtum*
Petals: shape	Narrowly obovate without claws	Broadly obovate with conspicuous claws
size posterior (mm)	8,0–15,0 (11,0) × 1,5–3,5 (2,5)	7,0–11,5 (9,5) × 3,5–8,0 (5,5)
size anterior (mm)	7,5–14,0 (10,0) × 2,0–2,5 (2,0)	6,0–11,0 (9,0) × 1,5–4,0 (3,0)
Stamens: max. length (mm)	4,5–11,0 (7,5)	4,0–6,0 (5,5)
Spur: length (mm)	5,0–12,0 (8,0)	2,5–5,5 (4,0)
Pedicel: length (mm)	2,0–8,0 (4,5)	1,0–4,5 (2,0)
Stipules: length (mm)	2,0–6,0 (4,0)	7,0–15,0 (10,0)
fixture	Basally attached	Decurrent along petiole for at least ½ their total length
Leaf: Petiole: length (mm)	5–22 (13)	7–70 (29)
permanency	Persistent	Semi-persistent, usually only evident within 30 mm of stem apex
Lamina: size (mm)	6–21 (11) × 4–13 (7)	15–47 (32) × 7–22 (15)
Indumentum:	Very shortly hirsute	Hirsute

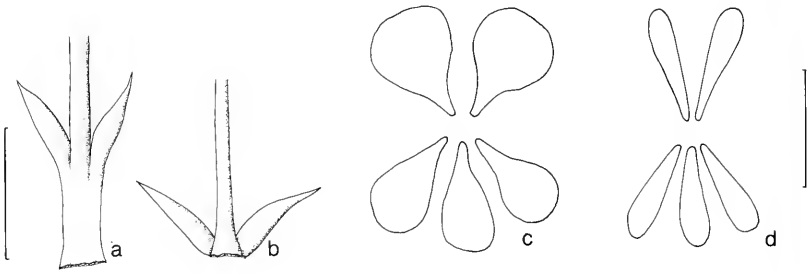

FIG. 1.
a and b, stipules of *Pelargonium hirtum* (*Drijfhout 2386* in STE-U *2189*) and *P. oreophilum* (*Van der Walt 549* in STE-U *807*) respectively; c and d, petals of *P. hirtum* (*Schlechter 5232*) and *P. oreophilum* (*Schlechter 8650*) respectively. Scale denotes 10 mm.

The following specimens are representative of the two species:

P. oreophilum

CAPE—3118: Brandewynrivier (-DD), *Schlechter 10824* (BOL!; Z!).
—3119: Nieuwoudtville (-AC), *Leipoldt s.n.* in BOL *10454* (BOL!).
—3219: Pakhuisberg/Pakhuispas (-AA), *Bolus 8944* (BOL!), *Esterhuysen 21724* (BOL, 2 sheets!; PRE, 2 sheets!), *Leipoldt s.n.* in BOL *20759* (BOL!), *Schlechter 8650* (BOL!; E!; PRE, 2 sheets!; Z!; type of *P. oreophilum*), *8657* (GRA!), *van der Walt 549* (STE-U!); Clanwilliam (-BB), *Leipoldt s.n.* in BOL *1409* (BOL!).

P. hirtum

CAPE—3218: Piquetberg (-AD), *Schlechter 5232* (Z!); Clanwilliam (-BB), *Leipoldt 470* (BOL!); Brackfontein at Clanwilliam (-BC), *Ecklon & Zeyher 540* (W, 2 sheets!); 9 miles from Velddrif on road to St. Helena Bay (-CC), *Thompson 800* (PRE!).
—3317: Saldanha (-BB), *Parker 4636* (BOL!).
—3318: Langebaan (-AA), *Grant 4702* (PRE!); Hopefield (-AB), *Bachmann 1537* (Z!), *2095* (Z, 2 sheets!); Darling (-AD), *Bolus 12630* (BOL!; PRE!), *Esterhuysen 23363* (BOL!; PRE!); Cape Town (-CD), *Dümmer 117* (E!); Lion's Head, *Pillans 3916* (PRE!), *Schlechter 1361* (Z, 2 sheets!), *van der Walt 475* (STE-U!), *Wilms 3073* (Z!), *Wolley Dod 1564* (BOL!); Lion's Rump, *Prior s.n.* in PRE *56353* (K, not seen; PRE!), *Thode 5994* (STE!), *7799* (STE!), *Zeyher 4769* (BOL!); Sea Point, *Bolus 4255* (BOL!), *Dümmer 370* (E!); Signal Hill, *Phillips 723* (PRE!); Paarl (-DB), *van der Merwe 1002* (PRE!; STE!); Brackenfell (-DC), *Bos 424* (PRE!; STE!); Tigerberg, *Krauss 1297* (W!); "near Groenekloof and Paarl" (-?), *Drège 1295* (PRE!).
—3418: Llandudno (-AB), *Hafström & Acocks 736* (PRE!).

SYNONYMY AND TYPIFICATION OF *P. RIBIFOLIUM* JACQ.

It has become evident that the names *Pelargonium ribifolium* Jacq. and *P. populifolium* Eckl. & Zeyh., which were both upheld as valid in Knuth's account of the Geraniaceae in Pflanzenr. **4,** 129 (1912), apply to a single species. The older name is *P. ribifolium*, which is therefore the correct name to apply to this species. *P. ribifolium* is typified by a specimen in Vienna (W) on which the name is written in Jacquin's handwriting. This specimen is here considered to be the holotype, and has been identified by us with a label to that effect. The correct citation is therefore as follows:

Pelargonium ribifolium Jacq., Icon. Pl. Rar. **3:** 11, t. 538 (1794). Type: without precise locality, no collector stated (W, holo.!).
P. populifolium Eckl. & Zeyh., Enum. **1:** 81 (1835). Type: CAPE—"'Zuureberge' prope 'Enon' (Uitenhage) eorumque ad 'Langekloof' (Georg)", *Ecklon & Zeyher 632* (S!; SAM!).
P. trilobatum sensu Eckl. & Zeyh. l.c., non Schrad. (1809) (teste *Ecklon & Zeyher 633* (S!)).

DELIMITATION OF *P. ABROTANIFOLIUM* (L.F.) JACQ.

The names *Pelargonium abrotanifolium* (L.f.) Jacq. and *P. incisum* (Andr.) Willd. apply to a complex of populations which are characterized by small, repeatedly dichotomously divided leaf laminae which are hairy and glandular to various degrees. In habit these plants are profusely-branched shrublets, occasionally reaching a height of 1 000 mm but more often c. 300 mm high. The flowers are sessile or extremely shortly pedicelled and decidedly zygomorphic, the petals are subequal in size and seven of the stamens are fertile. Due to the close morphological similarity between the plants, especially in respect of the leaves, the application of the names became problematic, for which reason a closer investigation was undertaken.

This material is characterized by straight, short stamens and pistil which are only 5–6 mm long; cuneate or narrowly obovate, plane petals which are dark purple to white with purple markings on the upper two; and leaves with adpressed hairs which lend them a more or less silvery appearance. These specimens exhibit a considerable variation in respect of colour of the petals, length of the spur, number of flowers per inflorescence, degree of division of the leaves, and hairiness. Superficially two groups can be distinguished:

The one group has leaves which are imperfectly divided to varying degrees with the extreme condition approaching that of the second group (see below). The midribs of the leaf segments are often externally visible as adaxial grooves. The leaves are hairy to varying degrees, from almost glabrous to visibly villous with adpressed white hairs, and grey-green in colour. The inflorescences consist of (usually) 1–3 flowers. The petals are mostly white, and the spur is 25–30 mm

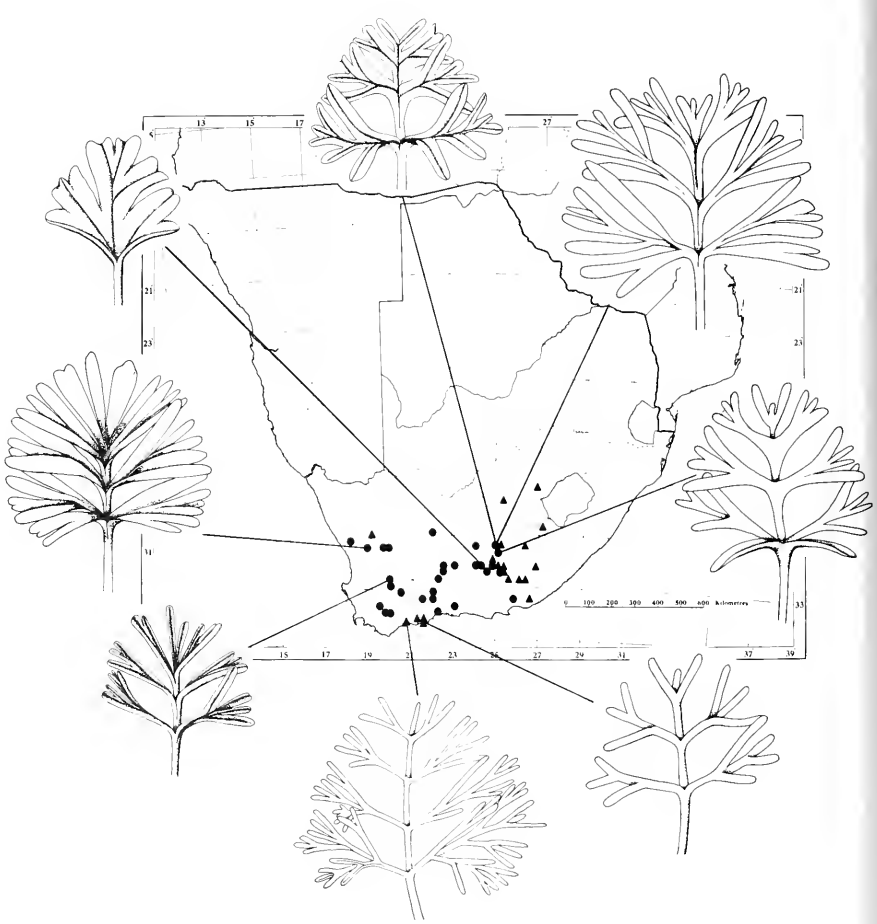

FIG. 2.
Pelargonium abrotanifolium: variation in leaf shape over known distribution range, drawn from live specimens cultivated in Stellenbosch.: ● *P. abrotanifolium* sensu stricto; ▲ "*P. incisum*".

long. The geographical range of this group of specimens more or less coincides with the winter rainfall region of the Cape, south of S 30°45′ and west of E 25°30′. We are of the opinion that the name *P. abrotanifolium* (L.f.) Jacq. applies to this group. The name *Geranium abrotanifolium* L.f. is typified by a sheet (LINN 858.19) which consists of two leafy twigs and a few badly-preserved flower fragments. While little information can be gleaned from the flower remains, the leaves fall within the range of variation recorded for this group.

The second group is characterized by leaves which are very finely divided into linear, involute segments of which the midribs cannot be distinguished externally. The leaves are rather densely villous with adpressed white hairs which lend a silvery appearance to the leaves. The inflorescences consist of up to five flowers. The petals are mostly pink to purple in colour, and the spur is 15–20 mm long. This group occurs immediately east of the first group, in an area receiving scant summer rainfall. The naming of this group presents a problem. The name *Geranium incisum* Andr. is not typified by a specimen, but by a coloured illustration in Andrews's *Botanist's Repository* **1:** t. 67 (1799). The leaves on this illustration appear to be similar to those of the present group, but the flowers are white with dark pink markings on the two posterior petals. White is not a typical colour for the petals of this group, but it does occur. We can therefore only conclude that *Geranium incisum* was based on an unusual form of this group.

The close morphological similarity between the two groups appear to indicate a mutual relationship closer than that of separate species. At a first glance it would appear that a case exists for recognizing *P. abrotanifolium* and *P. incisum* as subspecies of the same species on account of the geographically significant morphological variation. However, there appears to be a complete gradation between the two types of leaves to such an extent that it is practically impossible to draw a definite line between the two, especially when working with herbarium specimens. Furthermore, it is not always possible to correlate the colour of the petals, number of flowers per umbel and length of the spur with leaf characteristics.

It appears probable to us that the observed variation indicates a degree of genetical heterogeneity or genetical instability. It may be that the two forms are in the process of becoming geographically and reproductively separated from each other, but at present we consider it more practical to treat them as a single variable species to which the name *Pelargonium abrotanifolium* (L.f.) Jacq. applies, while *Pelargonium incisum* (Andr.) Willd. (*Geranium incisum* Andr.) is reduced to a synonym under the former.

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We wish to express our appreciation to Dr. D. J. B. Killick of the Botanical Research Institute in Pretoria for valued advice regarding the note on *P. sericeum*, and to Mrs. E. Vorster of our team for preparing the illustrations.

We are indebted to Miss E. M. Marais who pointed out to us that the name *Pelargonium auritum* should replace *P. hirsutum*.

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MANGROVE SOILS OF THE BEACHWOOD AREA, DURBAN

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Abstract

Soil samples from almost pure *Avicennia marina* (Forsk.) Vierh. and *Bruguiera gymnorrhiza* (L.) Lam. stands were characterized for their physical and chemical properties. All soils examined were weakly acidic, high in clay, organic matter, and moisture at saturation. Acidity increased with air drying. The soils were characterized by low bulk densities, moderate exchange acidities and high CEC. The predominant cations were sodium and magnesium. The ratio of sodium and magnesium to exchangeable bases was very high. The soils were low in available phosphorus and soluble sulphate. Generally, *Avicennia* soils were higher in pH, organic matter, CEC, exchangeable bases and lower in clay, exchange acidity and aluminium than *Bruguiera* soils.

Uittreksel

WORTELBOOMGRONDE IN DIE BEACHWOODGEBIED, DURBAN

Die fisiese en chemiese eienskappe is bepaal van grondmonsters van twee standplase waarop feitlik uitsluitlik *Avicennia marina* (Forsk.) Vierh. en *Bruguiera gymnorrhiza* (L.) Lam. voorkom. Die gronde wat ondersoek is, het swak suurgehalte, 'n hoë klei en organiese materiaal inhoud en 'n hoë voginhoud by versadiging gehad. Die suurgehalte het tydens uitdroging verhoog. Die gronde is gekenmerk deur lae massa digtheid, matige uitruilsuurgehaltes en 'n hoë kation uitruilkapasiteit. Die dominante katione was natrium en magnesium. Die verhouding van natrium en magnesium tot uitruilbare base was baie hoog. Die beskikbare fosfor en oplosbare sulfaat was laag. In die algemeen was die *Avicennia* gronde hoër in pH, organiese materiaal, kation uitruilvermoë, uitruilbare base en laer in kleigehalte, uitruilsuurgehalte en aluminium as die *Bruguiera* gronde.

Introduction

Mangrove vegetation occurs along many of the estuaries on the east coast of South Africa extending as far south as East London, S 33 ° (Macnae, 1962). In these estuaries mangroves occur up to the extreme tidal limit at high spring tides. The distribution of mangroves in intertidal zones is influenced by factors such as salinity, drainage, soil, water currents and climate. Several of these factors were reviewed recently (Chapman, 1976).

Mangrove species show a characteristic zonation within the swamp (Chapman, 1940; Hind, 1954; Bourdeau & Adams, 1956; Thom *et al.*, 1975). In the Beachwood marsh area the primary mangrove species is *Avicennia marina* which occupies the seaward portion of the swamp. The only other important mangrove species is *Bruguiera gymnorrhiza* which usually occurs on the landward side of the *Avicennia* zone.

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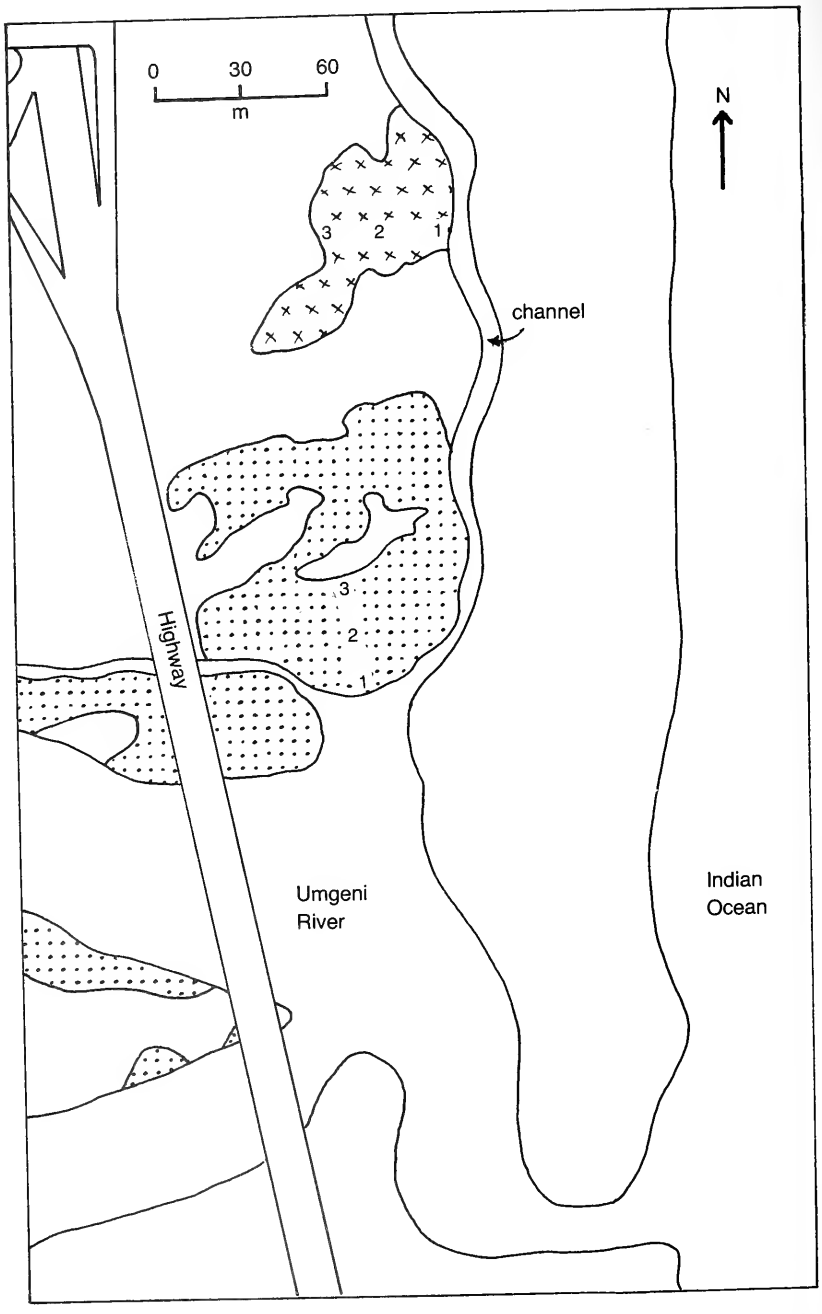
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m
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Distinct zonation patterns in mangrove communities locally have been attributed to various factors with little or no experimental verification. The ecology of mangrove communities has been studied in greater detail in other countries. Many of these studies were reviewed by Chapman (1976).

In this paper mangrove soils have been characterized to determine their possible role in influencing the establishment of distinct zones of mangrove species and to indicate the effect of mangrove species upon the soil. In addition, the nature of mangrove soils in South Africa has received little or no attention from research workers. It is hoped that this study will provide information which will be useful not only in understanding the ecology of our local mangrove communities but also in the conservation and management of our rapidly depleting mangrove areas.

The Study Area

The Beachwood area is located at the Umgeni River estuary, which is about 6 km to the north of Durban Bay. The mangrove area, situated on coastal sand dunes, is about 120 000 m^2 in extent. The area is drained by a channel which runs from a freshwater source in the north to the Umgeni estuary in the south (Fig. 1). The marsh is usually subject to tidal inundation twice daily. The mean tidal range is about 1,5 metres.

The climate in this area is warm temperate according to Köppen's classification. The mean annual temperature is 20,5 °C and the mean annual rainfall is 1 008 mm. The slope throughout the marsh is less than one degree.

Methods

Soil samples were collected from almost pure stands of *A. marina* and *B. gymnorrhiza*. In each mangrove area samples were collected from three sites along a transect 15, 30 and 45 metres from the edge of the channel (Fig. 1). All samples were air dried, ground with a pestle and mortar, passed through a 2 mm sieve and stored in glass bottles.

The following analytical procedures were used: particle size distribution by the hydrometer method (Bouyoucos, 1962); pH of field-moist and air-dried samples on 1:1 soil to water suspension using a glass electrode (Jackson, 1958); moisture at saturation (Bower & Wilcox, 1965); exchange acidity by extraction with barium acetate and titration with NaOH; aluminium by the aluminon method (Yuan & Fiskell, 1959); acetate soluble sulphate (Bardsley & Lancaster, 1965); organic matter by the Walkley-Black method (Jackson, 1958) and available

Fig. 1.
Map of part of the Beachwood mangrove area showing the distribution of mangroves (⋮⋮⋮⋮⋮ predominantly *Avicennia*, ⌃⌃⌃⌃⌃ predominantly *Bruguiera*) and the sampling areas (1, 2, 3).

phosphorus extracted with sulphuric acid containing ammonium sulphate and determined by the chlorostannous-reduced molybdophosphoric blue colour method (Jackson, 1958). Exchangeable cations were extracted with 1N ammonium acetate at pH 7. Concentrations of K, Mg and Ca in the extracts were determined by atomic absorption. Sodium was determined by flame emission spectrometry. Bulk density was measured using a steel cylinder with a volume of 772 cm^3. The cation exchange capacity was obtained by summation of the exchangeable bases and exchange acidity.

Results and Discussion

Particle size distribution and bulk density

The particle size distribution of mangrove soils (Tables 1 and 2) was similar throughout all profiles. There was an increase in sand content in the seaward edge of the *Avicennia* zone (profile 1).

All other profiles had a heavy texture. Most horizons were classified as clays. Lower down the profile the sand content increased suggesting the approach to the underlying sand dunes. The high sand content of profile 1 in the *Avicennia* zone could be attributed to the turbulent and churning action of the tidal waters which only permitted the coarse soil fraction to settle out of suspension. Part of the sand

Table 1.
Particle size distribution of *Avicennia* soils.

Layer	Depth mm	Particle size distribution %				Textural class
		Coarse sand	Fine sand	Silt	Clay	
			Profile 1			
1	0–200	86	4	4	6	sand
2	200–400	34	20	14	32	sandy clay loam
3	400–600	32	22	16	30	sandy clay loam
4	600–800	32	34	12	22	sandy clay loam
5	800–1 000	34	22	18	26	sandy clay loam
			Profile 2			
1	0–200	19	3	24	54	clay
2	200–400	28	2	24	46	clay
3	400–600	19	23	20	38	clay loam
4	600–800	15	35	18	32	sandy clay loam
5	800–1 000	11	27	22	40	clay
			Profile 3			
1	0–200	13	10	30	47	clay
2	200–400	7	10	24	59	clay
3	400–600	5	24	20	51	clay
4	600–800	3	20	30	47	clay
5	800–1 000	14	45	2	39	sandy clay

TABLE 2.
Particles size distribution of *Bruguiera* soils.

Layer	Depth mm	Particle size distribution %				Textural class
		Coarse sand	Fine sand	Silt	Clay	
			Profile 1			
1	0–200	5	13	38	56	clay
2	200–400	4	16	26	54	clay
3	400–600	14	6	22	58	clay
4	600–800	3	19	20	58	clay
5	800–1 000	36	28	14	22	sandy clay loam
			Profile 2			
1	0–200	3	15	26	56	clay
2	200–400	11	9	26	54	clay
3	400–600	4	38	22	36	clay loam
4	600–800	13	25	22	40	clay
5	800–1 000	4	18	18	60	clay
			Profile 3			
1	0–200	16	1	26	57	clay
2	200–400	4	9	22	65	clay
3	400–600	7	6	24	63	clay
4	600–800	10	39	16	35	sandy clay
5	800–1 000	19	44	10	27	sandy clay loam

probably originated from wind-blown material from adjacent sand dunes. *Avicennia* is the pioneer species at Beachwood and is able to colonise sandy substrates. Colonisation results in consolidation and stabilization of the substrate. This in turn permits the accretion of finer particulate matter such as silt and clay. Once the nature of the substrate is altered sufficiently, not only by *Avicennia* colonisation, but also by other soil forming processes, *Bruguiera* becomes established. The particle size distribution suggests that greater deposition of finer sediments is occurring further away from the water's edge. The high proportion of fine soil fractions in the surface layers of the *Bruguiera* zone (Table 2) is probably due to the slow rate of inundation of the swamp and to the low slope which allows water to remain in the swamp for prolonged periods. Most of the silt and clay that is deposited in the swamp originates from the coastal rivers and the off-shore sea.

The bulk density values were low and ranged from 1,41 g cm^{-3} to 0,61 g cm^{-3} (Tables 3 and 4).

The high bulk density in the surface layer of profile 1 of the *Avicennia* zone was due to the sandy nature of the soil. The low bulk densities in the remaining profiles are a reflection of the high clay and organic matter contents. The high clay content indicates that the soils have a high water-holding capacity and poor

TABLE 3.
Bulk density pH and moisture at saturation of *Avicennia* soils.

Layer	Depth mm	Bulk density g cm^{-3}	pH (H_2O)		Moisture at saturation %
			Field moist	Air dry	
		Profile 1			
1	0–200	1,41	6,3	6,1	32,7
2	200–400	0,87	6,4	5,9	37,6
3	400–600	0,97	6,2	5,7	35,3
4	600–800	1,08	6,0	5,8	25,8
5	800–1 000	0,95	6,1	5,8	28,7
		Profile 2			
1	0–200	0,88	5,6	5,3	40,5
2	200–400	0,73	5,7	5,5	40,6
3	400–600	0,73	5,7	5,3	34,2
4	600–800	0,91	5,8	5,5	33,5
5	800–1 000	0,79	5,8	5,7	37,2
		Profile 3			
1	0–200	0,75	5,9	5,2	42,5
2	200–400	0,67	5,9	5,3	42,4
3	400–600	0,97	5,8	5,3	36,9
4	600–800	0,61	5,8	5,3	38,9
5	800–1 000	0,84	5,8	5,4	35,4

TABLE 4.
Bulk density, pH and moisture at saturation of *Bruguiera* soils.

Layer	Depth mm	Bulk density g cm^{-3}	pH (H_2O)		Moisture at saturation %
			Field moist	Air dry	
		Profile 1			
1	0–200	1,01	5,9	5,5	39,2
2	200–400	0,95	5,8	5,2	39,4
3	400–600	0,85	5,8	5,5	38,3
4	600–800	0,82	5,9	5,5	37,2
5	800–1 000	0,93	6,0	5,4	32,1
		Profile 2			
1	0–200	1,01	5,6	5,2	38,0
2	200–400	0,95	5,6	5,4	38,3
3	400–600	0,86	5,7	5,2	29,7
4	600–800	0,88	5,8	5,3	34,5
5	800–1 000	0,84	5,9	5,3	37,6
		Profile 3			
1	0–200	0,95	5,7	5,2	37,2
2	200–400	0,84	5,8	5,4	37,2
3	400–600	0,88	5,8	5,5	37,6
4	600–800	1,05	6,0	5,5	33,4
5	800–1 000	0,98	5,4	5,4	29,5

drainage. The moisture content at saturation was high for both mangrove zones (Tables 3 and 4). These physical properties, together with the intermittent salinity, suggest that the soils have a low agricultural potential.

Acid properties

Soils from all profiles were moderately acid (Tables 3 and 4). Field moist pH values in the *Avicennia* zone ranged from 5,6 to 6,4 while in the *Bruguiera* zone the range was from 5,6 to 6,1. Generally, soils in the *Bruguiera* zone were slightly more acidic than in the *Avicennia* zone. In all horizons the pH values decreased with air drying. Air dry pH values ranged from 5,2 to 6,1 in the *Avicennia* zone and from 5,2 to 5,5 in the *Bruguiera* zone. This study confirms previous reports that drainage and reclamation of mangrove areas produce acid soils (Fleming & Alexander, 1961; Pons & Pons, 1974; Coultas & Calhoun, 1976; Van Breemen, 1976).

The exchange acidity of *Avicennia* soils was lower than that of *Bruguiera* soils (Tables 5 and 6).

In *Avicennia* soils the exchange acidity ranged from 3 to 5,7 me/100 g while in *Bruguiera* soils the range was from 5 to 7,4 me/100 g. In all soil profiles the exchange acidity generally increased with depth. The aluminium content of *Avicennia* soils ranged from 0,08 me/100 g to 0,28 me/100 g (Table 5). In

TABLE 5.
Acid properties of *Avicennia* soils.

Layer	Depth mm	Exchange acidity me/100 g	$A\ell^{3+}$ me/100 g	Soluble SO_4^{2-} me/100 g
		Profile 1		
1	0–200	4,3	0,15	0.04
2	200–400	3,0	0,19	0,15
3	400–600	4,0	0,21	0,16
4	600–800	5,0	0,23	0,24
5	800–1 000	5,7	0,28	0,25
		Profile 2		
1	0–200	4,0	0,08	0,12
2	200–400	3,6	0,20	0,26
3	400–600	4,7	0,21	0,19
4	600–800	5,1	0,24	0,14
5	800–1 000	5,4	0,27	0,16
		Profile 3		
1	0–200	4,2	0,15	0,17
2	200–400	3,9	0,19	0,17
3	400–600	4,9	0,20	0,30
4	600–800	5,0	0,21	0,23
5	800–1 000	5,4	0,28	0,27

TABLE 6.
Acid properties of *Bruguiera* soils.

Layer	Depth mm	Exchange acidity me/100 g	$A\ell^{3+}$ me/100 g	Soluble SO_4^{2-} me/100 g
		Profile 1		
1	0–200	5,0	0,23	0,10
2	200–400	5,6	0,26	0,11
3	400–600	5,8	0,30	0,17
4	600–800	6,4	0,29	0,18
5	800–1 000	7,4	0,31	0,17
		Profile 2		
1	0–200	5,0	0,24	0,11
2	200–400	6,2	0,24	0,14
3	400–600	6,7	0,26	0,25
4	600–800	6,9	0,27	0,18
5	800–1 000	7,2	0,28	0,24
		Profile 3		
1	0–200	5,1	0,17	0,12
2	200–400	5,5	0,21	0,16
3	400–600	6,0	0,25	0,12
4	600–800	6,7	0,28	0,16
5	800–1 000	7,1	0,31	0,12

Bruguiera soils the aluminium content was higher, the range being from 0,21 me/100 g to 0,31 me/100 g (Table 6). Soluble sulphate levels were variable in both mangrove zones (Tables 5 and 6). Generally subsoils contained higher levels of sulphate than the surface layers. Aluminium, sulphate and hydrogen ions were probably the main contributors to the exchange acidity.

Organic matter

Surface layers of all profiles were high in organic matter (Tables 7 and 8).

Generally the organic matter content decreased with depth within each profile. In the *Avicennia* zone the organic matter content increased with distance landwards. This was due to the greater density of *Avicennia* inland. The dense pneumatophores in the *Avicennia* zone probably trapped leaves and other debris thereby contributing to high organic matter. *Avicennia* soils had higher organic matter contents than *Bruguiera* soils. *Bruguiera*, unlike *Avicennia*, does not produce pneumatophores which are able to trap debris during tidal inundation. The darker soil colour observed with distance landwards is probably a reflection of the high organic matter content. High soil organic matter in intertidal swamps is usually associated with a slow rate of silting (Moorman & Pons, 1974).

TABLE 7.

Organic matter, cation exchange capacity, exchangeable cations and available phosphorus of *Avicennia* soils.

Layer	Depth mm	Organic matter %	CEC me/100 g	Exchangeable cations (me/100 g)				Available P ugml^{-1}
				Ca	Mg	K	Na	
			Profile 1					
1	0–200	4,6	23,7	3,3	3,4	1,0	11,7	0,30
2	200–400	3,6	54,3	4,2	18,5	1,6	27,0	0,63
3	400–600	2,8	44,6	3,9	16,4	1,2	19,1	1,20
4	600–800	2,5	42,6	5,1	9,4	1,4	21,7	1,13
5	800–1 000	3,2	50,7	6,0	15,2	1,6	22,2	0,33
			Profile 2					
1	0–200	5,4	56,0	3,0	21,3	2,0	25,7	0,55
2	200–400	4,8	65,6	4,5	23,4	2,3	31,8	0,55
3	400–600	3,9	60,2	3,6	24,6	2,5	24,8	0,50
4	600–800	3,9	57,2	3,4	17,6	2,0	29,1	0,25
5	800–1 000	3,9	57,5	4,5	19,7	1,8	26,1	0,55
			Profile 3					
1	0–200	6,3	72,8	4,3	25,0	2,3	37,0	0,65
2	200–400	5,4	83,3	5,1	25,8	3,3	45,2	0,45
3	400–600	4,8	75,8	5,6	25,8	2,5	37,0	0,38
4	600–800	4,9	77,4	4,7	25,8	2,8	39,1	0,53
5	800–1 000	4,1	69,0	5,0	21,3	2,5	34,8	0,13

TABLE 8.

Organic matter, cation exchange capacity, exchangeable cations and available phosphorus of *Bruguiera* soils.

Layer	Depth cm	Organic matter (%)	CEC me/100 g	Exchangeable cations (me/100 g)				Available P ugml^{-1}
				Ca	Mg	K	Na	
			Profile 1					
1	0–200	4,9	47,6	3,2	17,4	2,0	20,0	0,25
2	200–400	3,7	49,6	2,0	16,8	2,1	23,1	0,28
3	400–600	4,4	60,4	3,8	17,2	3,6	30,0	0,60
4	600–800	4,8	51,3	3,5	14,4	2,2	24,8	0,68
5	800–1 000	2,4	46,7	1,4	18,9	1,2	17,8	0,65
			Profile 2					
1	0–200	3,8	49,5	2,6	17,2	1,6	23,1	0,53
2	200–400	3,6	50,8	2,4	16,8	1,5	23,9	0,73
3	400–600	3,6	41,0	1,4	12,3	0,6	20,0	0,78
4	600–800	3,4	53,4	2,4	15,6	1,5	27,0	0,65
5	800–1 000	3,5	67,6	3,5	17,4	2,5	37,0	0,50
			Profile 3					
1	0–200	4,7	48,9	3,4	17,2	1,5	21,7	0,35
2	200–400	4,5	58,0	2,8	15,6	2,3	31,8	0,25
3	400–600	4,0	55,4	2,4	17,2	2,0	27,8	0,20
4	600–800	3,4	54,7	1,7	16,8	1,7	27,8	0,48
5	800–1 000	2,5	58,6	1,6	14,4	1,6	33,9	0,18

CEC, exchangeable cations and phosphorus

All soil profiles had high cation exchange capacities (CEC). In *Avicennia* soils the CEC ranged from 23,7 to 83,3 me/100 g (Table 7). The CEC generally increased with distance landwards in the *Avicennia* zone. This was probably a reflection of the trends in organic matter and clay contents. Generally *Bruguiera* soils had lower CEC than *Avicennia* soils, the range being from 41 to 67,6 me/100 g (Table 8). The high CEC of both mangrove soils suggests that these soils have a potentially high sink for cations. All soils contained large amounts of exchangeable sodium and magnesium (Tables 7 and 8). The ratio of exchangeable sodium and magnesium to extractable bases was very high probably because of the high concentration of sodium and magnesium in sea water. Soils inundated by tides equilibrate to have higher concentrations of exchangeable sodium and magnesium than upland soils (Coover *et al.*, 1975). The moderately acidic nature of the soils suggests that much of the calcium and magnesium is present in the form of sulphates. Generally, *Bruguiera* soils were lower in sodium, magnesium, calcium and potassium than *Avicennia* soils (Tables 7 and 8). This is primarily due to the proximity of *Avicennia* soils to the sea. *Avicennia* soils are more frequently inundated by saline water than *Bruguiera* soils. With distance landwards there is also greater dilution from freshwater sources.

In both mangrove soils, available phosphorus levels were low, the levels being higher in *Bruguiera* soils. At the acid pH values reported for these soils phosphorus was probably fixed by iron and aluminium. Air drying of the moist soil decreased the pH and increased phosphorus fixation. Low phosphorus levels in mangrove soils were reported by Huynh-cong-Tho & Egashira (1976).

General

In both mangrove zones great difficulty was experienced in obtaining deep sub-surface samples with the soil corer. The high water table limited the sampling depth to 1 m. Both mangrove soils showed very little profile differentiation up to this depth.

Unfortunately, pedological descriptions of the soil profiles were not undertaken for two reasons: firstly, as a result of the high water table holes dug in the marsh were completely filled with water within a few minutes; secondly the Beachwood area is a proclaimed nature reserve so that disturbance in collection of soil samples was kept to a minimum.

The data obtained for Beachwood soils differ markedly from those reported for a mangrove swamp in the Sydney district, Australia, by Clark & Hannon (1967). The soils in Sydney were predominantly sandy, surface and sub-surface samples comprising more than 75 % coarse sand. Clay content was less than 5 %. In the present study the clay content was as high as 59 % in the *Avicennia* zone and 65 % in the *Bruguiera* zone. Moorman & Pons (1974) and Pons & Pons (1974) reported

that mangrove soils in South America were predominantly clayey in texture and that very little coarse material was deposited in the mangrove proper. In West Malaysia the mangrove sediments were also found to be clayey (Diemont & van Wijngaarden, 1974). The coastal areas around Sydney are probably backed by sandy formations which could explain the high sand content. Clark & Hannon obtained high pH values (5,5 to 7,3) probably because of the presence of calciferous shell particles in the sand and extremely low CEC (0,38 to 0,84 me/100 g). Exchangeable bases were not determined by the Australian workers apparently because of the low CEC.

This study has revealed important differences between *Avicennia* and *Bruguiera* soils, although these differences were not subject to statistical analyses. Generally, *Avicennia* soils were higher in pH, organic matter, CEC, exchangeable bases and lower in clay, exchange acidity and aluminium than *Bruguiera* soils.

The composition of mangrove sediments probably differs in different areas and is determined to a large extent by various geogenetic parameters. These include factors such as climate, mineralogy of adjacent coastal areas and frequency of tidal inundation.

Although differences do exist between soils in the *Avicennia* and *Bruguiera* zones it is doubtful if these differences alone determine distinct zones of mangrove species. Differences in soil properties must be considered in relation to the habitat variables such as physiography, climate, salinity, soil drainage, water currents and salt spray. This conclusion is supported by the findings of Diemont & van Wijngaarden (1974) that there is a good relationship between vegetation and frequency of flooding, physiography and soil properties in the tidal areas of West Malaysia.

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SOME CHARACTERISTICS OF LEAF AND INFLORESCENCE PRODUCTION OF *STRELITZIA REGINAE* AIT. IN PORT ELIZABETH

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ABSTRACT

Differences in leaf and inflorescence production were found between two cultivated populations of *Strelitzia reginae* in Port Elizabeth. Although these differences could have been due to a number of factors, it is postulated that they were brought about by differences in light regime. The plants of one population were subject to prolonged periods of shading, especially during the winter months. In comparison to plants at a more exposed site, these plants showed decreased leaf and inflorescence production as well as a shorter flowering season. It is possible that low levels of solar energy suppress the development of primordia into inflorescences.

UITTREKSEL

SEKERE KENMERKE VAN BLAAR EN BLOEIWYSE ONTWIKKELING VAN *STRELITZIA REGINAE* AIT. IN PORT ELIZABETH

Verskille in die blaar en bloeiwyse ontwikkeling tussen twee gekweekte bevolkings van *Strelitzia reginae* in Port Elizabeth is gevind. Alhoewel die verskille die gevolg van 'n aantal faktore kan wees, word dit gepostuleer dat dit die gevolg van verskille in die lig regime was. Die plante van een bevolking was, veral gedurende die winter, onderhewig aan lang skaduweeperiodes. In vergelyking met plante in 'n meer blootgestelde terrein het hierdie plante verlaagde blaar en bloeiwyse ontwikkeling getoon, sowel as 'n korter blomtyd. Dit is moontlik dat die lae sonergie vlakke die ontwikkeling van primordia in bloeiwyses onderdruk.

INTRODUCTION

The brilliant colouring and uncommon morphology of the flowers of *Strelitzia reginae* have made them exceptionally popular as cut flowers in the floristry industry. Plants are therefore cultivated in many parts of the world with the sole aim of producing inflorescences for both local and export markets.

Information on flower production of *S. reginae*, as well as on factors controlling flower production, is obviously of vital importance to growers. It is only recently that research on these aspects has been initiated (Halevy, Kofranek & Kubota, 1976). Further research, in the form of an international project, which is being co-ordinated by one of the authors (A.H.H.), has also been conducted. Surveys of leaf and inflorescence production have been made in various countries

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and it is hoped that an analysis of these data will contribute to a greater understanding of floral yield in *S. reginae*.

This article reports on the data collected from cultivated plants in Port Elizabeth. These data are of particular interest as this site is very close to naturally occurring populations of *S. reginae*, this species being indigenous to the Eastern Cape Province in the Republic of South Africa.

Material and Methods

Two surveys were conducted:

Detailed survey of leaf and inflorescence production

Data were collected over a period of two consecutive years from plants growing in a large bed in Settler's Park, Port Elizabeth.

To understand the procedures followed a brief explanation of the mode of leaf production and vegetative multiplication (as described by Dyer, 1972) is necessary. Leaves of *S. reginae* arise distichously from the root stock forming a "fan". This process is finite; after a certain number of leaves have been formed, two leaves emerge back to back as a result of dichotomous branching of the rudimentary stem axis. These two are the first leaves (i.e. the outermost) of two new shoots and subsequent distichous leaf production gives rise to two new fans. The older a plant (or clone) is, the more fans it contains. Inflorescences emerge, from time to time, from the axils of one or more leaves in a fan.

For the purpose of this survey, single fans on 12 different plants were selected on 1977–01–17. Using a latex emulsion paint, the leaves of each fan were numbered, with the oldest (outermost) leaf taken to be number 1. The prefix A was used for each of the leaf numbers of this fan. When leaves emerged back to back, they were labelled B1 and C1 with subsequent leaves of the new fans being labelled B2, B3, etc. and C2, C3, etc., respectively.

The plants were examined at fortnightly intervals during the subsequent two years. Dates on which leaves and inflorescences were visible for the first time were recorded. The length of each inflorescence (total of scape and spathe) was taken each fortnight. After appearance of the first flower, inflorescences were cut off at the base. The data for each plant were set out in graphic form as seen in Figure 1.

After completion of the survey, means and standard errors of the various parameters mentioned in the section on results were calculated. Mean dates of certain events (such as appearance of inflorescences) were calculated by finding the mean figure for the time in weeks (with the date of commencement of the survey taken as zero time) and then converting to the appropriate date.

Comparative survey of flowering at two sites

This survey was conducted over a period of one year commencing on 1978–01–16. Fifteen whole plants or clones (consisting of groups of fans) were

selected at each of two sites. The one site was in Settler's Park and plants were chosen from the same bed as the ones used in the first survey. The other 15 plants were selected from plants growing on a traffic island in the William Moffat Expressway. The two populations were a few kilometres apart and in both cases the plants were growing on the south-facing slopes of the Baakens River Valley.

The total number of leaves on each plant were counted at the commencement and completion of the survey. Inflorescences were counted when the first flowers had appeared, and marked with latex emulsion paint. The populations were visited at fortnightly intervals for this purpose. Means and standard errors for various parameters (see Table 2) were calculated.

Results

Detailed survey of leaf and inflorescence production

The data obtained from each plant were set out as is shown for one particular plant in Figure 1.

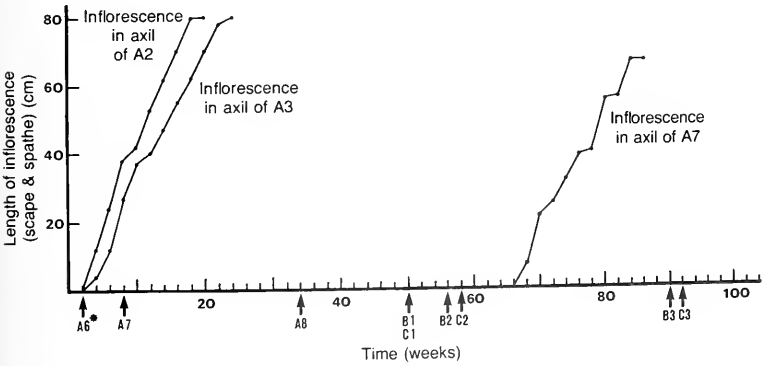

Fig. 1.
Emergence of new leaves and growth of inflorescences on a single fan of *Strelitzia reginae*. Dates corresponding to the time (in weeks) indicated on the abscissa are as follows: 0: 1977–01–17; 20: 1977–06–06; 40: 1977–10–24; 60: 1978–03–13; 80: 1978–07–31; 100: 1978–12–18.

*Emergence of newly differentiated leaves are indicated at the appropriate times below the abscissa. This particular fan had five leaves (A1 to A5) when selected at the commencement of the survey (1977–01–17).

It can be seen in Figure 1 that leaf production in this plant was confined to certain periods while at other times (between weeks 8 and 33, as well as between weeks 58 and 90) no new leaves appeared. This foliar dormant period was characteristic of all specimens in the survey and, on the average, extended over 25,3 (± 1,0)* weeks in 1977 and 26,2 (± 1,4) weeks in 1978. As can be seen from the mean dates in Table 1, this interval extended over the winter months.

TABLE 1

Mean dates for manifestation of some vegetative and floral characteristics of *S. reginae* plants in Settler's Park. (The standard error is shown in parenthesis.)

	1977	1978
Mean dates for foliar dormant period	March 31 (± 8 days) to September 22 (± 8 days)	April 18 (± 8 days) to October 18 (± 11 days)
Mean date of inflorescence emergence	January 27 (± 11 days)	January 15 (± 12 days)
Mean date of flower emergence	June 10 (± 16 days)	July 4 (± 20 days)

During the summer months, an average of 4,0 (± 0,1) new leaves were produced per fan with the mean time between the appearance of successive leaves being 9,0 (± 0,4) weeks.

Most fans produced only one inflorescence per growing season, with occasionally two differentiating. Where two differentiated this often took place simultaneously (as at week 4 in Fig. 1) or within a few weeks of each other. Mean value was 1,3 (± 0,2) inflorescences per fan for both 1977 and 1978.

Inflorescences emerged from leaf axils during midsummer (see Table 1). Average time taken from this point to emergence of the first flower out of the spathe was 20,0 (± 1,3) weeks in 1977 and 24,3 (± 2,0) weeks in 1978. The result is that although inflorescences appeared in midsummer, the show of blooms was concentrated in midwinter (see Table 1).

Over the two year period of this study, it was found that 3,2 (± 0,3) axils were infertile (i.e. did not bear inflorescences) between successive, inflorescence-bearing axils. Where two inflorescences were produced per flowering season, they were always from the axils of two successive leaves. Inflorescence production was synchronized in sister fans (i.e. fans produced by the two apical buds after dichotomous branching). This means that inflorescences were produced practically simultaneously from axils of corresponding leaves (say B2 and C2).

Leaves which bore inflorescences in their axils were, on the average, 42,7 (± 1,9) weeks old.

*Values for standard error are given in parenthesis.

Comparative survey of flowering at two sites

Four of the 15 plants in the Moffat Expressway selected for this survey were growing in the complete shade of young *Celtis africana* trees. This species is deciduous, which means that the four plants were exposed to more or less the same amount of solar energy during the winter months as the open-grown plants.

The selection of plants at this site was done at random and selection of four shaded plants was not intentional. However, summer shade seemed to have such a significant effect on growth that means for the two different groups are presented separately in Table 2.

TABLE 2

Some characteristics of leaf and flower production by *Strelitzia reginae* at two sites in Port Elizabeth. (The standard error is shown in parenthesis.)

	Settler's Park	Moffat Expressway	
		Summer shade	Exposed to full sunlight
Annual percentage increase in number of leaves/plant	14,99(± 2,55)	14,38(± 2,05)	43,79(±6,96)
Duration of flowering season (weeks)	15,2(± 2,4)	34,5(± 6,2)	39,0(± 3,7)
Flowering period (Mean dates)	1978–05–11 (± 9 days) to 1978–08–27 (± 15 days)	1978–03–13 (± 26 days) to 1978–11–13 (± 30 days)	1978–02–22 (± 11 days) to 1978–11–23 (± 22 days)
Ratio of number of inflorescences to number of leaves	0,145 ± 0,021	0,339 ± 0,015	0,339 ± 0,040

The data in Table 2 show that open-grown plants in the Moffat Expressway exhibited a three-fold greater increase in leaf number during 1978 than plants receiving summer shade or than those growing in Settler's Park.

Exposed plants had a slightly longer flowering season than plants in the shade, but both groups flowered over twice as long a period as plants in Settler's Park. The dates presented in Table 2 for flowering period are mean values for the first and last blooms to appear during the flowering season. The following observations which were made are also of significance.

(a) Not one of the survey plants in Settler's Park flowered before 1978–03–13 or after 1978–11–20 resulting in a distinct bloomless period in summer.

(b) There was not a single period during the year when blooms were not visible in the Moffat Expressway population. Although some of these plants

showed a distinct bloom-free period during the summer, five had open blooms during January and seven during December. Six of the Moffat plants did not exhibit a distinct flowering period but produced blooms on a continuous basis throughout the year. Only one of these was in a shaded position during summer.

An identical number of inflorescences per leaf were produced by exposed and shaded plants in the Moffat Expressway but the value for Settler's Park was less than half of this value.

Discussion

Strelitzia reginae plants growing in Settler's Park exhibited a very distinct growing and flowering season. Leaf production occurred only during the warmer half of the year while inflorescence production was concentrated to an even greater extent to the midsummer period. Actual opening of the blooms occurred mainly during winter as inflorescence growth took place over a period of five to six months.

This is probably not a universal pattern. Plants at the Moffat Expressway site tended to have a less distinct flowering period with blooms appearing throughout the year in this population. The ratio of number of inflorescences produced to number of leaves on these plants was more than double the value obtained from plants in Settler's Park. As mature *S. reginae* plants produce an inflorescence primordium in the axil of every leaf (Efrat-Lir, Halevy and Shoub, 1973) this implies that greater numbers of primordia in the Settler's Park population failed to develop into inflorescences than was the case at the Moffat site. Although this phenomenon could have been done to a number of factors it is postulated to be the result of lower levels of light energy received by the plants in Settler's Park. Although no measurements were made, it was very obvious that groves of tall trees to the north-east and south-west of this population resulted in extensive periods of shading in the mornings as well as in the afternoon, especially during the winter months. Halevy, Kofranek and Kubota (1976) have, in fact, demonstrated that shading can lead to reduced flowering in *S. reginae*. Low light energy is known to promote flower abortion or blasting in various species, possibly due to an effect on assimilate supply and distribution (Halevy, 1975; Sachs, 1977).

Although the few shaded plants at the Moffat site produced far less leaves and showed a shorter flowering period than the exposed plants at this site there was no difference in inflorescence yield between these two groups. Shading was, however, only experienced during the summer months and it could be that winter shading (which was particularly extensive in Settler's Park) is especially critical as regards inflorescence development.

The fact that virtually all the *S. reginae* plants growing in the wild are found on north-facing slopes (Van de Venter & Small, 1975) possibly reflects the

requirements of this species for high levels of solar radiation for growth and reproduction.

ACKNOWLEDGEMENT

The friendly co-operation of Mr A. Odgers, curator of Settler's Park, is appreciated.

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EUPHORBIA QUADRANGULARIS PAX AND A CLOSELY RELATED NEW SPECIES FROM TANZANIA

L. C. Leach*

Abstract

An amplified description of *Euphorbia quadrangularis* Pax of section *Tetracanthae* Pax is provided, its distribution as presently known recorded and its diagnostic characters discussed. A new closely related species from an adjacent but higher locality is described and illustrated.

Uittreksel

EUPHORBIA QUADRANGULARIS PAX EN 'N NAVERWANTE NUWE SOORT VAN TANZANIA

'n Vollediger beskrywing van *Euphorbia quadrangularis* Pax van die seksie *Tetracanthae* Pax word aangebied, die tans bekende verspreiding aangeteken en die diagnostiese kenmerke bespreek. 'n Nuwe naverwante soort van 'n naby geleë maar hoër vindplek word beskryf en geïllustreer.

Introduction

Euphorbia quadrangularis Pax, although not uncommon in Central Tanzania appears to be rather inadequately known; it is considered that an amplified description based on plants collected in that region, which appears to be the centre of distribution of the species, will be useful in connection with the publication of a closely related new species from an adjacent but higher locality.

Belonging in section *Tetracanthae* Pax, these two species, which often attain two metres or more in height, are by far the tallest in the section which is comprised mainly of shrublets less than one metre in stature.

Euphorbia quadrangularis Pax in Bot. Jahrb. **19:** 119 (1895), et apud Engler, Pflanzenw. Ost-Afrikas "C": 242 (1895), et in Bot. Jahrb. **34:** 84 (1904). Berger, Sukk. Euphorb.: 60 (1907). N.E. Br., Euphorbia in Flora Trop. Afr. **6**(1): 574 (1911). Brenan and Greenway, T. T. Check List: 212 (1949). Jacobsen, Handb. Succ. Pl. **1:** 469 (1960), et Lexicon Succ. Pl.: 228 (1947). Bjørnstad, Vegetation of Ruaha National Park: 32 (1976). Type: Tanzania, Itarige, *Fischer 519* (B; K, fragment with cyathia and drawing of type specimen).

Perhaps the most remarkable feature of this very distinctive species is its tall, very sparingly branched habit which is possibly most adequately described by the

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FIG. 1.
Euphorbia quadrangularis Pax.
Plants at Mbarika, Central Province, Tanzania, ± 2,5 m tall. *Leach and Brunton 10135.*

word ''lanky''. However, there are floral characters which are equally distinctive; amongst these, the minutely tuberculate glands separated by very shallow ''cuts'' and with a broad, eglandular, differently coloured margin, which is sometimes united to form a continuous circular rim around the disc-like glandular surface, is most noticeable, while the very broad, denticulate (not fimbriate), imbricate lobes seem to be diagnostic within the section.

Judging by the number of gatherings recorded by Bjørnstad, (*The Vegetation of Ruaha National Park*, Oslo, 1976), *E. quadrangularis* appears to be relatively common in the Ruaha National Park. Although I have been able to check the identification of only half the specimens cited there seems no reason to doubt the identity of the others. In *Richards 26376*, which seems to represent the greatest extent of variation, the glands of the involucre tend to be more distinctly separate in the somewhat smaller cyathia, but otherwise this specimen conforms very closely to the plants from Mbarika which are described above.

Plants have been found to be rather ''difficult'' in cultivation compared with those of most other species of *Tetracanthae*, the stems tending to rot at ground level (a tendency also noted by Dr. P. J. Greenway in specimens of his Mpwapwa gathering No. 2484, in cultivation at Mtotohovu).

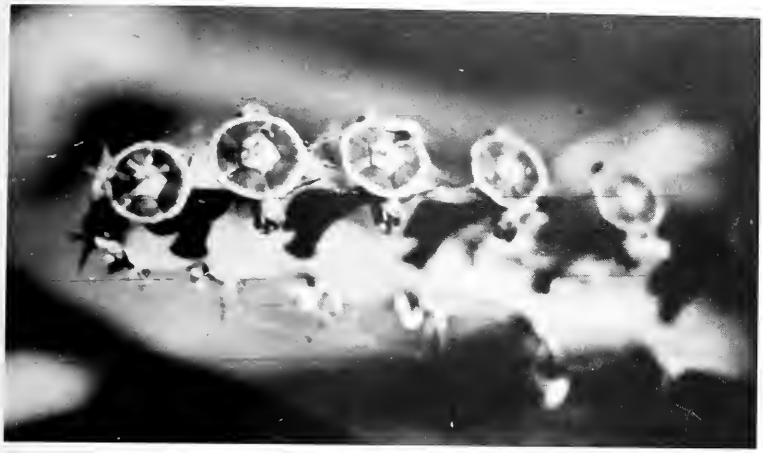

FIG. 2.
Euphorbia quadrangularis Pax.
Flowering branchlet showing flat, plate-like, subentire involucral glands. *Leach and Brunton 10135.*

Description: Based on plants at Mbarika (''Mtandika''), Iringa Distr., *Leach and Brunton 10135.*

Tall spiny shrubs, very sparingly branched, laticiferous, succulent, with an erect main stem 25–30 (40) mm thick towards the base, generally about 2 m, up to 3,5 m tall, with a few, usually opposite, widely spreading branches 10–15 mm thick, rarely, and only when damaged, branching freely from the base with a ''coppice growth'' of erect branches. *Stem* and *branches* greyish-green, slate-grey or purplish, usually mottled with darker shades, sometimes heavily so, particularly towards and on the angles, acutely 4-angled, with the sides flat or slightly concave and the angles sinuately tubercle-toothed with the teeth 1–3 mm high, 8–15 mm apart along the angles, and the long, narrow, decurrent spine shields forming a shortly interrupted or sometimes subcontinuous, brownish-cream or pale brown horny margin. *Spines* in divergent, horizontally spreading pairs at the apex of the tubercle teeth, 4–8 mm long, pale brown at the base becoming blackish towards the apex. *Leaves* broadly ovate-acute, caducous, leaving an inconspicuous, subcircular or depressed obovate leaf-scar 2–3 mm above the spine pairs, flanked by a pair of sharp prickles 1–2 mm long. *Inflorescence* a horizontally arranged, shortly pedunculate cyme of three cyathia, with the initial, central cyathium usually male deciduous or sometimes bisexual and the lateral bisexual cyathia borne on widely diverging, often oppositely spreading cyme branches. *Peduncle* bibracteate ± 3 mm long, 2 mm diam.; *bracts* more or less broadly ovate ± 2 mm wide, 1,25 mm

FIG. 3.
Euphorbia quadrangularis Pax.
Widely divergent bisexual cyathia, showing outwardly facing anthers and more nearly separated glands. *Leach and Brunton 10135*, in cult. Nelspruit.

long with a thickened, truncate, brown base. *Cyme branches* pale bluish to yellowish-green, minutely white puncticulate, sometimes flushed with purplish-red, ± 3,5–4 mm long, 2 mm diam.; *bracts* rose-pink, more or less obovate, sometimes subacute, minutely crenulate at the apex, truncate at the base, ± 1,75 mm long, 1,25 mm wide. *Involucre* pale green, similarly white puncticulate, shallowly, very broadly funnel-shaped (very thin and plate-like when viewed from the side), 8,5–9,5 mm diam. including the glands, ± 3 mm long; *glands* 5, very closely contiguous, separated only by shallow "cuts" not reaching the underside of the glands and sometimes not extending to the then entire margin above (the cyathium then rather reminiscent of that of *Synadenium grantii* Oliv.), yellowish to apple-green, flat, densely provided with small red-tipped papillae and copiously supplied with nectar, ± 5 mm × 2,5 mm with a broad, pale peach to dark red-purple in colour, eglandular, lightly radially rugulose margin, 0,5–0,75 mm wide, minutely crenulate-crisped on the subacute outer edge; *lobes* 5, broadly flabellate or more or less transversely oblong-elliptic, slightly 2-lobed, 3 mm broad, 1,5 mm long, irregularly denticulate, imbricate, pale green, minutely white puncticulate, rose flushed towards the apex, sometimes almost entirely rose coloured. *Male flowers* ± 15, arranged in 5 fascicles, each internally subtended by an irregularly laciniate denticulate bract ± 3 mm long and broad and provided with a number of variably laciniate, denticulate bracteoles; *pedicels* somewhat

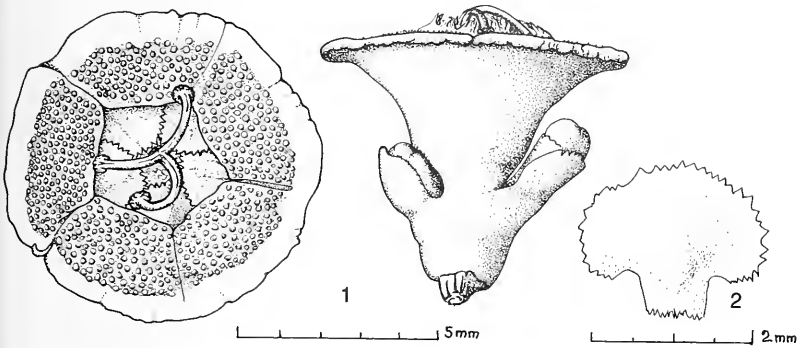

FIG. 4.
Euphorbia quadrangularis Pax.
1. Cyathium. 2. Involucral lobe from *Leach and Brunton 10135*.

translucent, ± 3,5 mm long; *filaments* ± 1,5 mm long, slightly spreading with the peach-coloured anther thecae turned outwards, with yellowish-cream pollen. *Female flower*, ovary included, more or less broadly obovoid, longitudinally 3-ribbed, supported on a somewhat 3-lobed pedicel-perianth ± 2 mm long; ovule suspended beneath an exceptionally large, hood-like finely fringed obturator; *styles* arising from a pedestal-like base at the apex of the ovary, ± 3 mm long, very shortly (up to ± 0,5 mm) united at the pale green base, spreading recurved, pinkish becoming dark red at the capitate, rugulose, simple, not at all bilobed or sometimes very slightly emarginate stigmas. *Capsule* (from plant in cultivation at Nelspruit 3.XI.1963) obtusely 3-lobed, green, heavily tinged on the angles and apex with dull red-purple and subdensely white puncticulate, ± 8 mm diam., 5 mm high, very shortly exserted on a stout, 4 mm long pedicel-perianth, obscurely pentagonal at its base ± 3 mm diam. at the middle gradually expanding towards the obscurely irregularly lobed perianth. *Seed* almost spherical, ± 2,75 mm diam., ash-grey, with whitish patches, covered with relatively large and well-spaced, somewhat flattish, whitish verrucae, with a small black pit at one end; suture brown.

MATERIAL EXAMINED

TANZANIA—T1: 81 mls from Mwanza on Musoma road, ± 4 000 ft. alt., 18.VII.1960, *Verdcourt 2899* (EA, K); T2: 49 mls W of Endulen, exceptionally large cyathia, 27.VII.1957, *Bally 11606* (EA, K); T5: Lake Kitengiri, near Chem Ohem Mission, 1 050 m alt. Singida Distr., 3.XI.1960, *Richards 13507* (K); Manyoni, upper scarp, ± 4 000 ft. alt., Dodoma Distr., 6.XII.1931, *Burtt 3510* (EA, K, PRE); Mpwapwa, fl. and fr. 27.IX.1948, *Hornby 2991a* (K, SRGH), ibid.

28.VIII.1930, *Greenway 2484* (EA, K, PRE), idem cult. Mtotohovu, 10.VIII.-1942, *Greenway 6607* (EA, K); Lake Nzuhe (''NZUI''), Mpwapwa Distr., 18. VIII. 1938, *Mr and Mrs Hornby 914* (EA, K, PRE); T7: Ruaha Nat. Park, *Richards 26376* (M); eastern Ruaha Nat. Park, Iringa Distr., 7.VIII.1970, *Thulin and Mhoro 631* (K); Gt. Ruaha Riv. ''Manganga-Madangu'' ± 2 600 ft. alt., 19.VIII.1969, *Greenway and Kanuri 13762* (K); Mbarika (''Mtandika''), ± 2 400 ft. alt., Iringa Distr. fl. 27.VI.1960, *Leach and Brunton 10135* (BR, K, LISC, MO, PRE, SRGH); Kimirimatonga Range, Iringa Distr., 3 500 ft. alt., 13.III.1970, *Greenway and Kanuri 14092* (K). Imprecise localities: ? T1: Itarige, *Fischer 519* (B, K, fragment and drawing of type). ? T5: N. Ukaguru, overlooking Masai Plains, Ibido-Gairo area *Silcock* sub *Bally E240* (EA, K, PRE, photo).

Specimens recorded as in EA are taken from a list of *Euphorbia* specimens held in Nairobi sent to me by Dr. P. R. O. Bally, and of which I have seen duplicates.

Euphorbia quadrilatera Leach, sp. nov. ad *E. quadrangularem* Pax proxime accedit sed frutice aliquanto liberius ramosa, ramis minus patulis, planta omnis praesertim inflorescentia vividius colorata manifeste discedens; cymis fere sessilibus, pedunculo cymarum ramisque crassioribus brevissimis, involucri glandulis concavis minutissime pusticulatis margine distincto lato carenti, stigmatibus aurantiacis, polline aurantiaco, capsula minore seminibusque minimis brunneis tuberculatis distinctissima.

Holotypus: Tanzania, Njombe Distr., *Leach and Brunton 10350* (SRGH).

Frutex erectus, laticiferus, succulentus, spinosus, usque 2 m vel ultra altus, caule in sectione quadrato aliquando demum subcylindrico, basin versus usque 4 cm crasso, primo saepe caule simplici usque 0,6 m alto, nonnunquam praecipue ubi laesus fruticem dense ramosum formans. *Rami ramulique* constanter quadrilateri, 10–25 mm crassi, acute angulati, lateribus viridibus plerumque leviter concavis angulisque infuscatis sinuato-dentatis, dentibus 2–5 mm altis, secus angulos 10–25 mm distantibus, aliquando dente minore in podario prope basin interposito; *podaria* longe anguste decurrentia, brunnea mox cinerascentia, marginem corneum interdum subcontinuum formantia, *spinis* binis divergentibus late patulis, plerumque c. 10 mm longis, basi brunneis, apicem versus nigrescentibus, ad apicem dentium tubercularium armata, aliquandoque spina singulari brevi acuto prope basin etiam instructa. *Folia* rudimentalia cito caduca; cicatrix subcircularis inconspicua spinulis binis acutis, 0,5–2 mm longis armata. *Inflorescentia* cymosa glabra; cymae singulares, axillares, fere sessiles; pedunculus brevissimus bibracteatus, bracteis plus minusve transverse anguste lunatis, c. 3 mm latis; cyathiis 3, horizontaliter dispositis; cyathium medium masculum deciduum vel raro

FIG. 5.
Euphorbia quadrilatera Leach.
Plant in cultivation Hort. Leach., Salisbury, *Leach and Brunton 10350*.

bisexuale; cyathia lateralia bisexualia, in cymarum ramis brevissimis portata, bracteis atrocarmesinis, subquadratis truncatis vel obtusissimis, c. 2 mm longis. *Involucrum* extus indistincte minute albido-puncticulatum, basi pallide viride supra flavescens, glandularum margine vivide carmesino, latissime plus minusve obconoideum, 8,5–9,5 mm diam. glandulis inclusis, c. 3 mm longum; *glandulae* 5, plus minusve transverse oblongae, c. 4,5 mm × 2 mm, arcte contiguae, concavae, minutissime pusticulatae, luteae anguste vivide carmesino-marginatae; *lobi* 5, arcte imbricati, plus minusve transverse late elliptici, aliquam 2-lobati, 2,5–2,75 mm lati, 1,5–2 mm longi, fimbriato-dentati fimbriis usque 0,5 mm longis, rubescentes usque atro-carmesini. *Flores masculi* c. 30, bracteolis filiformi-fimbriatis, in fasciculis 5 dispositi, fasciculus quisque bractea lata flabellata, fimbriata, laciniata, interne subtentus; *pedicelli* 2,5–3 mm longi; *filamenta* 1,25 mm longa. *Ovarium* plus minusve trigono-ovoideum, perianthio irregulariter leviter lobata c. 0,75 mm longo insidens; ovulum obturatore relative grandi bilobata suspensum. *Styli* graciles, subrosei, 3,5–4 mm longi, patuli-reflexique, basi breviter connati, aliquanto levissime ventricaliter sulcati, apicibus amplificatis

FIG. 6.
Euphorbia quadrilatera Leach.
Flowering branch of cultivated plant,
Salisbury.

rugulosis, raro levissime emarginatis, translucenti-aurantiacis. *Capsula* fere matura, trilobata angulis subacutis, c. 5 mm diam., 4 mm alta; *perianthio* tumidissimo, c. 3 mm diam., 1 mm longo, irregulariter 5-crenati. *Semen* late ellipsoideum, brunneum, tuberculatum, c. 2,5 mm × 2 mm.

A laticiferous succulent spiny *shrub*, up to 2 m or more tall, with a square-sectioned, erect main stem up to 40 mm thick towards the base, sometimes becoming subcylindric with age, often simple up to ± 0,6 m high, usually rather sparingly branched and rebranched above, occasionally when damaged forming quite large, densely branched shrubs; branches erectly spreading to spreading and the branchlets more widely spreading, 10–25 mm thick, strictly square-sectioned. *Stem* and *branches* green, marked with darker green, particularly along the angles, acutely 4-angled with the sides slightly concave and the angles sinuately tubercle-toothed, with the teeth 2–5 mm high, 10–25 mm apart along the angles, with the long, narrowly decurrent *spine shields* usually separated by the flowering eye or sometimes forming a subcontinuous horny margin, initially brown soon becoming grey. *Spines* paired, divergent, widely spreading, at the apex of the tubercle teeth, usually ± 10 mm long, brown at the base, becoming black towards the sharp apex; spine shields sometimes provided with a single sharp spine up to 1,5 mm

long at the apex of an intermediate small sinuation towards the base of the spine shield shortly above the flowering eye. *Leaves* caducous, leaving a small, very inconspicuous subcircular scar, flanked by a pair of sharp prickles 0,5–2,0 mm long, 2,0–3,5 mm above the main paired spines. *Inflorescence* a horizontally arranged, very shortly pedunculate cyme of three cyathia with the initial central cyathium usually male deciduous or rarely bisexual; the lateral cyathia bisexual, borne on very short stout cyme branches. *Peduncle* bibracteate, ± 1,5 mm long, up to 4,5 mm thick; *bracts* more or less lunate, ± 3,0 mm wide, 0,75 mm long. *Cyme branches* bibracteate, pale green, minutely whitish puncticulate 2,0–2,5 mm long, ± 3,0 mm thick; *bracts* dark red-purple, subquadrate or semi-circular, ± 2 mm long, truncate or obtuse, somewhat obtusely denticulate (scarcely crenulate). *Involucre* outside pale green becoming yellowish above and dark red on the outer margin of the glands, rather obscurely minutely whitish puncticulate, shallowly broadly obconic, 8,5–9,5 mm diam. including the glands, ± 3 mm long; *glands* 5, more or less transversely oblong, ± 4,5 mm × 2,0 mm, closely contiguous, deep yellow, dark red-purple on the outer margin, concave, very minutely pusticulate (not tuberculate and lacking the broad, differentiated margin of the closely related *E. quadrangularis*); *lobes* 5, closely imbricate, more or less transversely broadly elliptic, slightly 2-lobed, 2,5–2,75 mm × 1,5–2,0 mm, deep rose to dark red-purple, fimbriate toothed with fimbria up to 0,5 mm long. *Male flowers* ± 20–30, provided with a number of filiform, fimbriate bracteoles, arranged in 5 fascicles, each internally subtended by a broad, fimbriate, lacerate bract, ± 2,5 mm long; *pedicels* more or less colourless, 2,5–3,0 mm long; *filaments* rose coloured, 1,25 mm long; *anthers* peach coloured with orange pollen. *Ovary* more or less obtusely, trigonously ovoid, seated on an irregularly slightly lobed perianth

FIG. 7.
A comparison of seeds of *E. quadrangularis* (central) and *E. quadrilatera* on each side.

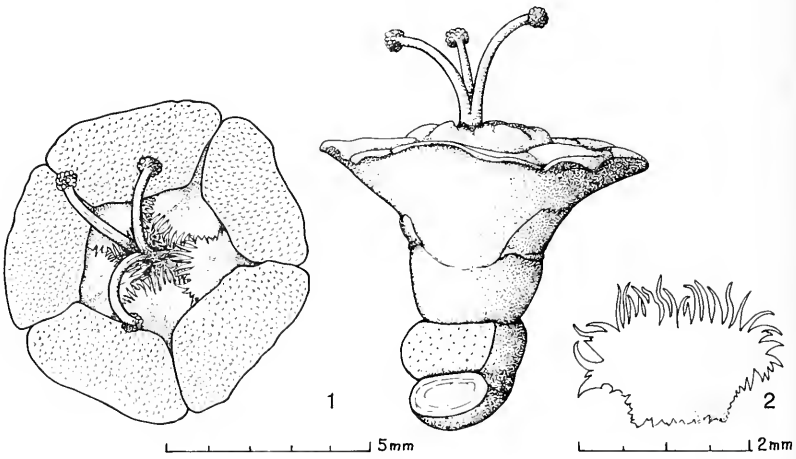

FIG. 8.
Euphorbia quadrilatera Leach.
1. Cyathium. 2. Involucral lobe from *Leach and Brunton 10350*.

± 0,75 mm long; *ovule* suspended beneath a relatively large 2-lobed crenulate obturator. *Styles* slender, pink, 3,5–4 mm long, spreading recurved, shortly united at the base, very slightly sulcate down the inner face, with the enlarged, rugulose, translucent-orange apices usually entire, rarely slightly emarginate. *Capsule* almost mature, subacutely three-lobed, ± 5 mm diam., 4 mm high; *perianth* becoming much swollen in fruit, unequally 5-crenate, ± 3 mm diam., 1 mm long. *Seed* broadly ellipsoid, brown, tuberculate, ± 2,5 mm × 2,0 mm.

E. quadrilatera is very closely related to *E. quadrangularis* which occurs in adjacent areas of Tanzania but at generally lower altitudes; it differs from that species, however, in a number of significant characters. In habit the new species is rather more freely but less divaricately branched and the differently textured epidermis is much brighter in colour; however, it is in the flowering and fruiting characters that the greatest divergencies are to be observed. The cymes of the new species are almost sessile compared with the relatively stipitate cymes of *E. quadrangularis*, while its brightly coloured, concave, very minutely pusticulate glands are very different from the tuberculate, widely smooth-bordered glands of its relative, as are also its fimbriate lobes (denticulate in Pax's species); although of short duration the orange stigmas and pollen of *E. quadrilatera* are also quite distinctive, and finally its capsule is considerably smaller, as are the quite different, more nearly ellipsoid, tuberculate brown seeds.

A tendency for the main stem to become somewhat enlarged at ground level, after the manner of that of the related *E. subsalsa* Hiern and a new species from Kasama, was noted in both wild and cultivated plants.

E. quadrilatera is relatively easy to cultivate, as well as to propagate from cuttings, in marked contrast to the difficulties usually experienced with *E. quadrangularis* in cultivation, a trait which was also remarked upon by Dr. P. J. Greenway, in notes attached to specimens of this species in cultivation at Mtotohovu.

Although so far recorded only from the type locality where good regeneration was evident with plants of all ages relatively plentiful, it seems probable that other gatherings from the same general region will prove to belong here, but I have not seen the material.

Material Examined

TANZANIA—T7: Njombe Distr., near Makambako; plants frequent in dwarf *Brachystegia* woodland, c. 5 500 ft. alt., fl. 27.VII.1960, and fr. Hort. Leach, 9.X.1972, *Leach and Brunton 10350* (K, PRE, SRGH), fl. 14.IX.1969 (BR, MO).

The abbreviations used for herbaria are as listed by P. K. Holmgren and W. Keuken, *Index Herbariorum, Regnum Vegetabile* 92 (1974).

Geographic divisions, "T1" etc. are as used for *Flora of Tropical East Africa*.

Acknowledgements

My grateful thanks are due to:

The Directors of BR, K, M, and PRE, for the loan of valuable material and for the facilities of their herbaria when these have been visited, and to Dr. P. R. O. Bally for a list of *Euphorbia* specimens held in the East African Herbarium, Nairobi.

Jl S. Afr. Bot. 46 (3): 325–328 (1980)

Book Reviews

PHYSIOLOGICAL ECOLOGY OF THE ALPINE TIMBERLINE TREE EXISTENCE AT HIGH ALTITUDES WITH SPECIAL REFERENCE TO THE EUROPEAN ALPS, by W. Tranquillini, translated from the German by U. Benecke, with pp. xi + 137, 67 figures and 21 tables. ISBN 3–540–09065–7. Berlin, Heidelberg, New York: Springer-Verlag, 1979. Volume 31 in the series "Ecological Studies: Analysis and Synthesis", edited by W. D. Billings, F. Golley, O. L. Lange and J. S. Olson. Cloth DM 54, US $29.70.

The latest in this admirable series of substantially bound volumes based on decades of research work conducted over a range of plant formations, vegetation types and aquatic and terrestrial ecosystems. I remember reviewing the first of them in 1972; D. E. Reichle's *Analysis of temperate forest ecosystems*. It then cost R12,50. Its price today—R25! Tranquillini's perceptive "in depth" analysis is now R30,80.

One wonders how much longer we can continue to put up with this inflationary punishment. Admittedly, these ecologically-oriented volumes could be said to cater for a rather more "specialised" readership to whom the price may not be considered excessive, and most libraries can easily absorb the financial outlay. The less-affluent student, however, is finding the going very rough indeed. From my own experience, it is becoming very difficult to prescribe books for undergraduate courses. Students are referred to library shelves and this inevitably engenders frustration. The "overnight" shelf is a poor substitute for personal possession. Publishers might address themselves to this very real and increasing stumbling block to scholarship.

Price notwithstanding, I doubt very much whether any other comparable volume offers such value on the ecophysiology of high-altitude forests in Europe. Judging from the extraordinarily comprehensive bibliography a mass of information has been utilised in its preparation. It is a pity, although the omissions are perfectly in accord with his terms of reference, that the author has only evaluated the literature on Alpine forest areas outside Europe. Research on the Afro-Alpine regions of this continent, the work of Webster, Kitamura and others in Afghanistan and the Himalayas are completely excluded.

The layout is a model of precision and clarity. After a brief review of the chief features of Alpine timberlines, in which emphasis is concentrated on climatic-altitudinal plant adaptive relationships, the remainder of the text is divided into six sections embracing natural regeneration, growth, dry matter production, water relations, stress factors and resistance, and a final synoptic chapter.

The scientific facts assembled not only provide insight into the physical environment and the life processes of the woody components of the spectra occurring in the Alps but also provide agriculture and forestry with a sound foundation for the conservation and restoration of forests in mountainous areas generally. It thus has a significance far beyond the immediate context of Europe. Even in Africa, if the full protective value of mountain forests is to be realised, similar ecophysiological studies will be an important adjunct to the more pragmatic methods of silviculture.

It is to be hoped that the absolute necessity for restoring our catchment areas is now appreciated in this country. The situation further north is almost beyond redemption. Nevertheless, as the wise man said "In the Kingdom of the Blind the one-eyed man reigns". The strength of a Sovereign State is composed of many facets. Our decision-makers would be well-advised to husband their resources and we are dealing here with the most important resource of all.

Dr. Tranquillini is to be congratulated on the compilation of a package full of concentrated meat. Many could find nourishment in it.

O. KERFOOT

PHYSIOLOGY OF MOVEMENTS, edited by W. Haupt and M. E. Feinleib, with pp. xvii + 731, 185 figures and 19 tables. ISBN 3–540–08776–1. Berlin, Heidelberg, New York: Springer-Verlag, 1979. Volume 7 in "Encyclopedia of Plant Physiology, New Series", edited by A. Pirson and M. H. Zimmermann. Cloth DM 198, US $108,90.

Movement is an obvious expression of life and the fact that it is less conspicuous in plants is due only to its slower—and to the inexperienced eye well nigh unobservable—occurrence in members of this Kingdom. Seen *in toto*, movement is a phenomenon which encompasses a spectrum so wide that even an encyclopaedic volume might not fully do it justice. So, for example, cohesion—and explosion-induced movements have had to be excluded from the book under review, and by far not all the tropistic and nastic movements have been covered.

In a book of this nature—to which 27 authors contributed 25 chapters—it is impossible to provide the Strasburger-type of integrated, comprehensive overview and, as increasingly seems to be the case, the respective treatments are presentations by individuals of their own highly specialized subject areas, with the integration undertaken by editors Haupt and Feinleib in the relatively short Introduction.

The physiology of movement, a research area dominated in the past by German botanists, is receiving wider international attention and although the names of some prominent workers (e.g. Kamiya, Bünning) do not feature among the contributors to this book, those of persons who have made significant contributions in this field do (e.g. Sweeney, Wilkins, Raschke, Johnsson). The subject matter falls into four basic parts: (1) locomotion in microbial plants, (2) intracellular movements, (3) turgor-based movements and (4) growth movements. Growth movements are discussed in terms of those directed by light and gravity, and those not directed primarily by stimuli of external origin.

Raschke's chapter on stomatal movement is excellent and particularly appropriate in view of the current interest in the mechanisms which control the opening and closing of the pore, and Johnsson's on circumnutation is an interesting discussion of models that might underlie this phenomenon.

Johnsson, known for his work on oscillatory water transport, is a physicist who is engaged in botanical research. Reading his chapter only underscores the notion that physics and mathematics undeniably are valuable complementary subjects to the study and better understanding of physiological botany.

This well-produced, well-researched treatise, with its extensive author and subject indices, is highly recommended for institutional library shelves as well as for those of the botanists interested in aspects of the physiology of movement from both research and teaching points of view.

CHRIS H. BORNMAN

PLANTKUNDE: ORGANOGRAFIE EN SITOLOGIE,* deur W. F. Reyneke, L. A. Coetzer en N. Grobbelaar, met pp. 133. Durban: Butterworths, 1979. R7,23.

Hierdie boekie is een van 'n reeks van vier teorieboeke en een praktiese handleiding wat deur dosente van die Departement Plantkunde aan die Universiteit van Pretoria geskryf is. Die reeks boekies dek die kursus vir Plantkunde I wat tans deur studente aan hierdie universiteit gevolg word. Die skrywers het van die veronderstelling uitgegaan dat die studente wat dit sal gebruik oor feitlik geen biologie-agtergrond beskik nie.

Die inhoud van die boekie is in tien hoofstukke verdeel. Hoofstuk 1 is inleidend van aard en gee onder andere 'n oorsig oor die ontstaan van lewe op die aarde, 'n verdeling van lewende organismes en 'n uiteensetting van die verskillende vakgebiede van die plantkunde.

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* Review first published in the *South African Journal of Science*.

Die orige nege hoofstukke is verdeel in die twee afdelings, organografie en sitologie. In die afdeling organografie word 'n oorsig oor die uitwendige bou van blomplante (Anthophyta) gegee. Daar is sewe hoofstukke waarin die bou en funksies van wortels, stingels, blare, bloeiwyses, blomme, vrugte en sade bespreek word. Die afdeling sitologie bestaan uit twee hoofstukke: in die eerste hoofstuk word daar 'n uiteensetting van die ultrastruktuur van die plantsel met sy membrane en organelle gegee, en in die laaste hoofstuk word mitose bespreek.

Die taalgebruik in die boekie is goed. Die beskrywings is op 'n sistematiese wyse uiteengesit en lees maklik. Tegniese terme verskyn in vetdruk sodat dit onmiddellik die aandag trek en die student sal help om dit te memoriseer. Die teks word uitstekend toegelig met sketse en foto's wat almal van 'n hoë gehalte is. Altesaam 143 figure is gebruik. Dit is veral verblydend dat die skrywers sover moontlik voorbeelde van Suid-Afrikaanse plante gebruik. Dit behoort die belangstelling in ons inheemse flora te stimuleer.

Die skrywers het met baie terme afgewyk van dié in die *Plantkundewoordeboek* van die Suid-Afrikaanse Akademie vir Wetenskap en Kuns. In sommige gevalle was dit geregverdig om af te wyk, maar in ander gevalle is daar myns insiens onnodige nuwe terme geskep. Die behoefte en noodsaaklikheid om die *Plantkundewoordeboek* te hersien, word dus weer eens onderstreep.

Enkele klein vakkundige foute is ook opgemerk. In hoofstuk 10 word daar byvoorbeeld gemeld dat mitose uit twee fases — kariokinese en sitokinese — bestaan, terwyl die algemene opvatting is dat mitose en kariokinese sinoniem is.

Alles in ag geneem, moet die skrywers en die uitgewer gelukgewens word met 'n puik werk wat die lig gesien het. Dit is 'n mooi bydrae tot die Afrikaanse vakliteratuur. Die boekie sal nie alleen vir universiteitstudente van groot waarde wees nie, maar sal ook met groot vrug deur biologie-onderwysers op hoërskole gebruik kan word.

J. J. A. VAN DER WALT

PRAKTIESE PLANTKUNDE,* deur W. F. Reyneke, P. D. F. Kok en N. Grobbelaar, met pp. 105. Durban: Butterworths, 1979. R7,23.

Hierdie handleiding vir eerstejaarstudente is die vyfde in 'n reeks van vier boeke wat die teorie dek en hierdie enkele volume vir die praktiese werk. Die werk voorsien in 'n lank gevoelde behoefte in die Departement Plantkunde aan die Universiteit van Pretoria, maar ook wyer aan Plantkunde-departemente aan ander opleidingsentrums. Soos die outeurs dit in die voorwoord stel, dek hierdie boek meer as wat gewoonlik in so 'n inleidende kursus aangebied word sodat dit met vrug gebruik kan word in kursusse waarvan die leerplanne effens anders daar uitsien.

Die belangrikste onderdele waaraan die outeurs aandag skenk, is die organografie en anatomie van wortels, stingels en blare, die bou van bloeiwyses en blomme, mitose, meiose en genetika, asook 'n studie van 'n aantal verteenwoordigers van die Monera, Protista, Fungi en Plantae.

Die tegniese versorging van die werk is van hoë gehalte, met slegs 'n paar uitsonderings, soos die foto's wat die gedeelte oor die ligmikroskoop illustreer. Die gebruik van 'n donkerder agtergrond om sekere gedeeltes te beklemtoon, is hoogs geslaag. Daar word slegs van illustrasies gebruik gemaak waar dit nodig is en studente word dus ook na ander werke verwys, wat die oorteken van sketse uit die handboek tot 'n minimum sal beperk. Lofwaardig is ook die pogings van die outeurs om die belangrikheid van die korrekte voorbereidings- en tekentegniek by die leser tuis te bring.

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* Review first published in the *South African Journal of Science*.

Die simbole wat by die konstruering van blomdiagramme en blomformules gebruik word, word duidelik geïllustreer saamgevat. Dit voorsien in 'n werklike behoefte en sal sekerlik wyer as net deur eerstejaarstudente gebruik word. Sommige terme wat gebruik word, mag hier en daar die leser se wenkbroue laat lig, maar al verskil die leser van die outeurs, is daar 'n aantal navolgenswaardige voorbeelde van sinvolle taalgebruik, byvoorbeeld die ietwat onbekende gebruik van *kieming* in plaas van die meer algemene (en miskien foutiewe) *ontkieming*.

Die groepering van die leerstof is soms vreemd, byvoorbeeld die bespreking van die gebruike van radioaktiewe isotope saam met die blaaranatomie, maar die optimale benutting van klastyd veroorsaak sekerlik dergelike situasies in enige kursus, waar dit ook al aangebied word.

Geen plantkundige aan enigeen van die instansies waar opleiding in die vak aangebied word, sal sonder sy eksemplaar van hierdie publikasie wil wees nie, en dit kan en sal sekerlik met groot vrug deur junior en selfs meer senior studente gebruik word.

Die outeurs moet gelukgewens word met 'n goed deurdagte publikasie wat slegs 'n positiewe bydrae tot die dosering van die vak kan lewer.

J. COETZEE

ANNOUNCEMENT

The publication is announced of EXCELSA 8 and EXCELSA TAXONOMIC STUDIES NO. 2 *(A review of Tridentea Haw. Asclepiadaceae)*. These are both obtainable from Excelsa, P.O. Box 8514, Causeway, Salisbury, Zimbabwe.

Jl S. Afr. Bot. 46 (4): 329–342 (1980)

STUDIES IN ORCHIDACEAE FROM SOUTH CENTRAL AFRICA

Graham Williamson
(Oranjemund, South West Africa)

Abstract

Six new species and one new variety of Orchidaceae are described from South Central Africa. All species are illustrated. The systematic affinities of all the taxa are discussed and distribution data are included.

Uittreksel

STUDIES VAN ORCHIDACEAE VANAF SUID-SENTRAAL AFRIKA

Ses nuwe soorte en een nuwe variëteit van Orchidaceae vanaf Suid-Sentraal Afrika word beskryf. Alle soorte word geïllustreer. Die sistematiese verwantskappe van alle taksa word beskryf en verspreiding word aangegee.

Habenaria (sect. Pentaceras) **debilis** Williamson, sp. nov., affinis *H. silvatica* Schltr. sed tota planta magis gracili, floribus nutans, calcari non tumido, stigmatibus non decurvatis differt (Fig. 1).

Typus: Zambia, *G. Williamson 1416* (SRGH, holotypus; K, isotypus).

Herba terrestris usque 200 mm alta. *Tubera* elongata ovoidea, 10 mm longa, 6 mm diametro. *Caulis* erectus gracilis, per totam longitudinem foliatus, teres, circiter 5 mm diametro. *Folia* usque 9, 4 basalia vaginiformia, 4 media lineara lanceolata acuta, folio maximo 55 mm longo, 5 mm lato, folia suprema bracteiformia. *Inflorescentia* usque 50 mm longa, 18 mm lata, usque 11—flora laxiscula; bracteae lanceolatae ovario floribus longiores, maximo 10–50 mm longo, 4 mm lato, *ovarium* et *pedicellus* usque 10 mm longum, 2 mm latum, ovarium curvatum prorsum. *Sepalum* intermedium convexum 90 °e caule axe, ovatum obtusum vel subacutum, 5,2 mm longum, 3,6 mm latum; *sepala* lateralia deflexa oblongo-ovata acuminata, 6 mm longa, 2 mm lata. *Petala* ad basin bipartita; lobus posticus, horizontalis, sepalo dorsali plus minusve adhaerens, anguste linearis, 5 mm longus, 0,8 mm latus, acutus vel obtusus; lobus anticus falcatus linearis, porrectus, 3,2 mm longus, 0,5 mm latus, acutus. *Labellum* tripartitum, basi indiviso, 1,0 mm longo, lobo medio lingulato pendens, usque 5,6 mm longo, 1,0 mm lato, obtuso; lobis lateralibus recurvatis linearibus, 3 mm longis, 0,4 mm latis, acutis; *calcar* dependens cylindricum non tumidum et non tortum, 7 mm longum, apice rotundato. *Anthera* semi erecta, 1,2 mm alta, rotundata, canalibus porrectis gracilibus, 0,8 mm longis, *auriculis* lobatis 0,6 mm

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longis; *stigmata* porrecta plus minusve clavata, fere 1–1,8 mm longa; *rostelli* lobo intermedio triangulari, 0,5 mm alto, obtuso.

Habitat: Wet well-shaded *Brachystegia* woodland growing in white sandy soil.

Critical remarks: *Habenaria debilis* is closely related to *H. silvatica* Schltr. but differs in that it is a much smaller more slender plant with nodding flowers. The ovary lies closer to the stem and the bracts usually extend above the flowers. The anterior lobe of the petal is much shorter than the posterior lobe and the lateral lobes of the labellum are much shorter than the middle lobe. The stigmatic processes unlike *H. silvatica* Schltr. are not recurved.

The specific epithet is derived from the rather weak, miserable, nondescript appearance of the plant.

ZAMBIA: Northern Prov.: Shiwa Ngandu approx. 8 km west of homestead, Feb. 1969, *G. Williamson 1416* (SRGH, holotype; K, isotype).

Habenaria (Sect. Diphyllae) **kabompoensis** Williamson, sp. nov., affinis *H. leucotrichae* Schltr., a quo petalis lobis anticis longioribus, labello lobis longioribus, calcari breviore apice inflato, rostello lobo intermedio aequato alto antheris loculis differt (Fig. 2).

Typus: Zambia, *G. Williamson et B. K. Simon 1766* (SRGH, holotypus; K, isotypus).

Herba terrestris, 130–200 mm alta; *tubera* ovoidea, 10 mm longa, 10 mm diametro, tomentosa. *Caulis* erectus gracilis, teres, non robustus; per totam longitudinem subdense hirsutis longiusculis, crispis, albidis, 4–5 mm longis; folio singulo basali humistrato instructo; folio caulino singulo bracteaforme. *Folium* basale prostratum, ovato-orbiculare, 30 mm longum et latum, apice acuto, basi cordato; supra subdense pilis inclinatis albidis, usque 5 mm longis; margine valde dense pilo-ciliatis; *folium* caulinum lanceolatum acutum, usque 11 mm longum, subdense hirsutum. *Inflorescentia* laxe 6—flora, 80 mm longa, fere 30 mm diametro; bracteae lanceolatae acuminatae, 8 mm longae, 3 mm latae subdense hirsutae. *Flores* patens sub-erecti, sepala viriduli, ceteri albi; *pedicellus* cum *ovario* leviter arcuatus, usque 10 mm longus. *Sepalum* intermedium erectum valde concaviuum, ovatum acutum, 7,2 mm longum, 3 mm latum, extra pagina semidense pilis; *sepala* lateralia patentia oblique curvatim semi-ovata, 8 mm longa, 2,8 mm lata, extra paginae semi-dense pilis. *Petala* fere ad basin bipartita; partitio postica erecta, sepalo intermedio adhaerens, lineari-lanceolata acuta, 6–8 mm longa, 0,5–0,7 mm lata; partitio antica linearis, fere filamentosa curvatum extrinsecus sursum, 18–20 mm longa, 0,3–0,7 mm lata. *Labellum* fere ad basin tripartitum; partitiones laterales curvatim extrinsecus sursum lineares subacutae, 18–20 mm longae 0,5–0,9 mm latae; partitio intermedia pendens, linearilingulata, obtusa, 12–14 mm longa, 1 mm lata; *calcar* dependens, cylindratum,

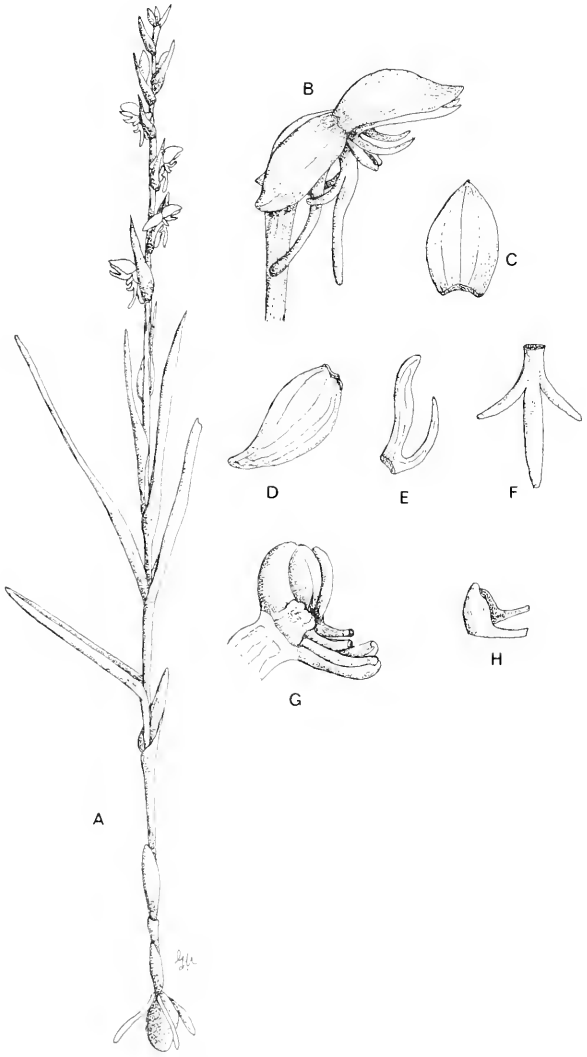

FIG. 1.
Habenaria debilis. A, habit, × $^2/_3$; B, flower, × 3; C, dorsal sepal, × 3; D, lateral sepal, × 3; E, petal, × 3; F, labellum, × 3; G, column × 14; H, rostellum, × 15; (all magnifications approximate). All from *G. Williamson 1416*.

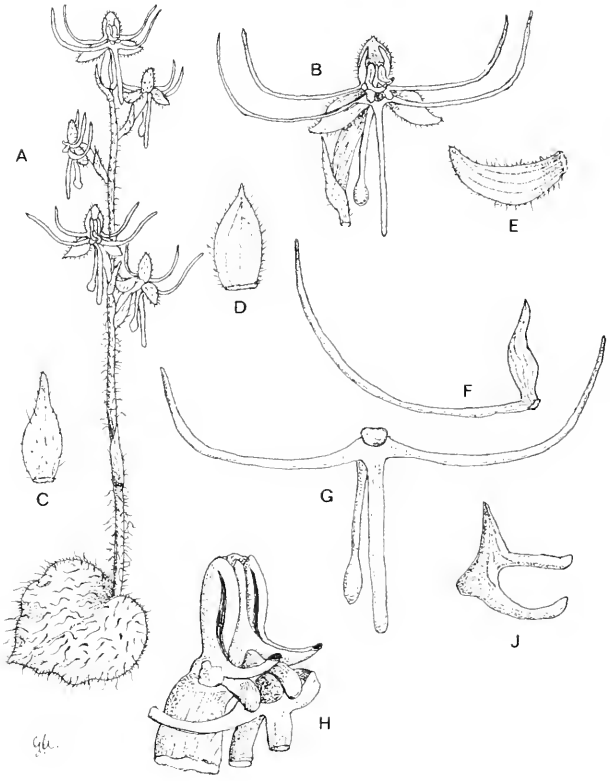

FIG. 2.
Habenaria kabompoensis. A. habit, × $^{2}/_{3}$; B, flower, × $1^{3}/_{5}$; C, flower bract, × 2; D, dorsal sepal flattened, × 2; E, lateral sepal flattened, × 2; F, petal, × 2; G, labellum, × 2; H, column, × 7; J, rostellum, × 7; (all magnifications approximate). All from *G. Williamson and B. K. Simon 1766*.

plus minusve parallelum ovario, 8–11 mm longum, apice tumore, 1,3–1,5 mm diametro. *Anthera loculis* erectis, canalibus porrectis, 2 mm longis; *auriculis* ovatis, 0,8 mm longis; stigmata deflexim curvata, crassiuscule plus minusve complanata; rostellum trilobulata, lobo intermedio 2 mm alto, aequato antheris loculis alto.

Habitat: In woodland, growing in leafmould on quartzite ridge or on laterite.

Critical remarks: *Habenaria kabompoensis* resembles *H. leucotricha* Schltr. but differs in possessing much longer lateral petal lobes and longer lateral lobes of the labellum. The spur in the new species is also shorter than the middle lobe of the labellum and the rostellum midlobe is shorter than the anther thecae.

ZAMBIA: Western Prov.: On quartzite ridge on east bank of Kabompo River, Dec. 1969, *G. Williamson and B. K. Simon 1766* (SRGH, holotype; K, isotype); between Kafue and Mushindamu River in scrub on laterite, Solwezi Dist., Jan. 1962, *W. Holmes 0322* (SRGH).

Stolzia repens (Rolfe) Summerh. in Kew Bull. **7:** 141 (1953). var. **obtusa** Williamson, var. nov., a *S. repens* (Rolfe) Summerh. typica sepalis et petalis valde obtusis distinguenda (Fig. 3).

Typus: Rhodesia, *J. S. Ball 1398* (SRGH, holotypus).

Habitat: High altitude moist evergreen shade forest.

Critical remarks: The new variety differs from the typical variety in that all the perianth members are more oblong with very obtuse apices; this is especially so with the petal shape. The flower is also smaller in comparison with leaf size than in the typical variety. *Stolzia repens* (Rolfe) Summerh. occurs at lower altitudes on *Brachystegia* trees while the new variety seems to replace the typical variety at higher altitudes in semi-montane moist mist forests.

RHODESIA: Eastern Prov.: N. and n.e. faces of Castle Beacon, Umtali, Jan. 1976, *J. S. Ball 1398* (SRGH, holotype).

Bulbophyllum carinatum Williamson, sp. nov., affinis *B. unifoliato* De Wild. sed labello marginato non serrato non papillato, basi alis et inferne pagina carinata differt (Fig. 4).

Typus: Mozambique, *Lady Drewe 33* (SRGH, holotypus).

Herba epiphytica glabra; *rhizoma* teres, circiter 2 mm diametro, sub pseudobulbis radices graciles caespitosis flexuosas griseas emittens, pseudobulbi 18–30 inter se distantes gerens. *Pseudobulbi* pyriformes, erecti 4-angulati, 20–26 mm alti, 8–10 mm diametro, flavido-virides, basi vagina scariosa vestiti, apice acuti monophylli. *Folium* lingulatum vel lanceolatum, 55–90 mm longum, 10–15 mm latum, obtusum. *Scapus* suberectus, usque 140 mm longus; *pedunculus* teres, 80–90 mm longus, 1,5 mm diametro, vaginis 4 arctis scariosis acutis, circiter 8 mm longis; *rachis* nutans teres 50–60 mm longus. *Flores* parvi, usque 20,

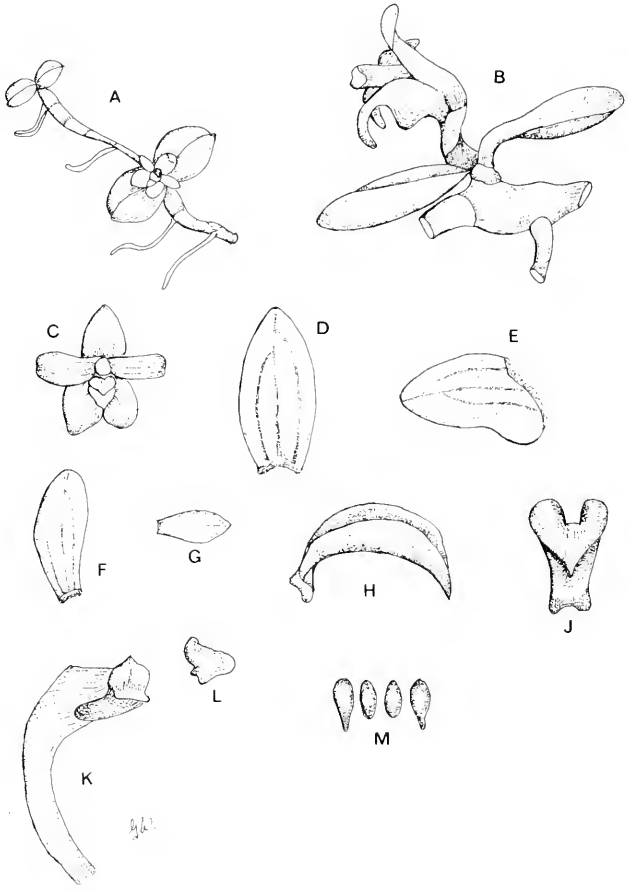

FIG. 3.
Stolzia repens var. *obtusa*. A, habit, × $1^2/_5$; B, flower and leaves, × 4; C, flower, × 3; D, dorsal sepal, × 5; E, lateral sepal, × 5; F, petal, × 5; G, labellum flattened, × 5; H, labellum side view, × 15; J, labellum front view, × 15; K, column without anther cap, × 13; L, anther cap, × 13; M, pollinia, × 26; (all magnifications approximate). All from *J. S. Ball 1398*.

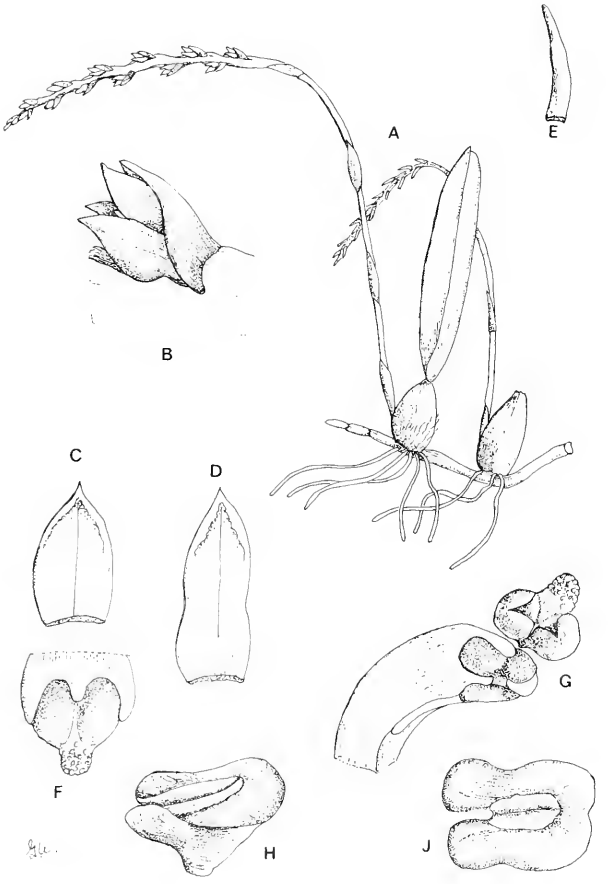

FIG. 4.
Bulbophyllum carinatum. A, habit, × $^{2}/_{3}$; B, flower, × 6; C, dorsal sepal, × 7; D, lateral sepal, × 7; E, petal, × 7; F, anterior portion of column from above, × 20; G, column ¾ front view with anther cap lifted, × 20; H, labellum ¾ side view, × 20; J, labellum from above × 20; (all magnifications approximate). All from *Lady Drewe 33*.

sessiles, alternati non resupinati, flavi-purpuro violaceis maculatis et purpurato labello; bractae ovatae, 3,5 mm longae, 3 mm latae, acutae, flore breviores; *ovarium* sessile, 1–2 mm longum. *Sepalum* intermedium concavum, ovatum, 3 mm longum, 1,3 mm latum, valde acutum; *sepala* lateralia lanceolata, in mediis constrictis, 4,2 mm longa, 1,5 mm lata, basibus crassis, apicibus acutis. *Petala* lanceolata, leviter falcata, 1,8 mm longa, 0,3 mm lata, acuta. *Labellum* naviculiforme, basi alis, apice obtuso, supera pagina duplicates cristis, infera pagina carinata, 1,4 –1,8 mm longum, 0,8–1,2 mm latum, carinatum, 0,4 mm altum. *Columna* leveter teres, brevis, 1 mm longa; *stelidia* lanceolata leveter falcata, 0,3 mm longa, obtusa; pes columnae leveter incurvatus, 2 mm longus; *anthera* pyriformis apice mammiforme papillato prorsum ultra stelidis, 0,8 mm lata.

Habitat: Riverine fringe forest and semi-montane forest.

Critical remarks: The new species is closely related to *Bulbophyllum unifoliatum* De Wild., but differs in that the lateral sepals and petals are much narrower. The lip is without papillae or serrations, is smaller and gives the appearance of a keeled boat. The specific epithet is derived from the presence of the keel located on the underside of the lip.

MOZAMBIQUE: Tsetserra, Jan. 1959, *Lady Drewe 33* (SRGH, holotype).

RHODESIA: Eastern Prov.: Chamanimani Mountains. Musapa gap. Jan. 1962, *J. S. Ball 986* (K).

Eulophia ecalcarata Williamson, sp. nov., ab. *E. eylesii* Summerh. et *E. nyasa* Rendle labello sine ornamento, non lobato et ecalcarato differt (Fig. 5).

Typus: Zambia, *Williamson 216* (SRGH, holotypus; K, isotypus).

Herba erecta terrestris, sub saprophytica, usque 370 mm alta; *tubera* elongato-elliptica multi-contorta ramosis, 70 mm longa, 15 mm diametro; radices e tubere ubique emissae, 1,5 longae. *Folia* usque 8, purpureo-brunneus, 6 basalia ad vaginis redacta ovato-lanceolata acuminata; 1–2 suprema ovata acuminata, usque 30 mm longa, 10 mm lata. *Scapus* 370 mm altus angulatis, ramosis, 9 mm latus, purpureo-viridi-brunneus. *Inflorescentia* usque 35-flora, densa, usque 200 mm longa; bracteae lanceolatae erectae, 7 mm–25 mm longae, 1,5 mm–5 mm latae, acutae vel acuminatae; *pedicellus* cylindraceus tortus, usque 5 mm longus, *ovarium* valde papillosum porcatum, viride, 25 mm longum, 5 mm diametro. *Flores* erecti, horizontali vel nutans, viriduli, rubro-venis. *Sepalum dorsale* anguste lanceolatum, 18 mm longum, 2 mm latum, acutum; *sepala lateralia* sepalo intermedio similia. *Petala* anguste ovata, 12 mm longa, 3 mm lata, acuta. *Labellum* petalis similia, non ornamentato, non lobato et ecalcarato. *Columna*

teres, 4 mm longa, 2 mm diametro; *operculum antherae* pyrifomis apice papillato; pollinia pyriformia, 0,4 mm longa; *viscidium* triangulare, angulis rotundatis, basi 0,4 mm latum.

Habitat: Sandy humus-rich soils in shaded *Brachystegia* woodland and on humus on quartzite outcrops.

Critical remarks: This interesting species is only known from two localities east of Lusaka. When first collected it was considered to be an abnormal form of saprophytic *Eulophia*. Due to the discovery of a second colony some miles further east of the first colony it was decided to describe the plant as a new species. It is quite remarkable in that the labellum has not even the slightest vestige of a spur. The plant does not display any abnormal features. The column is normally developed and the viscidium is present and normally formed. Fertilization is by self-pollination similar to many other *Eulophia* species in Zambia.

ZAMBIA: Central Prov.: 17 km east of Lusaka under *Brachystegia* trees in humus on quartzite outcrop, Jan. 1967, *G. Williamson 216* (SRGH, holotype; K, isotype); 20 km east of Lusaka in sandy humus-rich soil under shaded *Brachystegia* trees, Nov. 1974, *G. Williamson and A. Gassner 2326* (K).

Eulophia farcta Williamson, sp. nov., ab *E. nyasa* Rendle, labello latioro, lobis lateralibus brevibus, apice pauco densibus et valde brevi calcari differt (Fig. 6).

Typus: Zambia, *G. Williamson & B. K. Simon 1764* (SRGH, holotypus; K, isotypus).

Herba erecta, terrestris, subsaprophytica, usque ± 250 mm alta; *tubera* non visa. *Folium* caulinum lanceolatum, 12 mm longum, 5 mm latum, acutum. *Scapus* teres, usque 250 mm altus, 2,5 mm diametro, purpureo-brunneus. *Inflorescentia* densa, usque 120 mm longa, 40 mm lata, 16–20 flora; bracteae lanceolatae, 12 mm longae, 5 mm latae, acutae. *Pedicellus* cylindraceus tortis, usque 3,5 mm longus, *ovarium* valde papillosum vel verrucatis, porcatum, viride, 15 mm longum, 5 mm diametro. *Flores* horizontali vel nutans. *Sepalum dorsale* lanceolatum, 15 mm–17 mm longum, 3–4,5 mm latum, fere cuspidatum purpureo-brunneum. *Sepala lateralia* sepalo intermedio similia sed basibus dilatatis. *Petala* anguste ovata, 12–14 mm longa, 4–4,5 mm lata, alba-viride, rubro-venis, acuta fere cuspidata. *Labellum* naviculiforme medio trilobatum, cremeum, 15 mm longum, 7 mm latum; pars basalis tribus venis elevatis parallelis longitudinalibus viridirubris, venis ramosis purpuratis; lobi laterales breves, acuti; lobus medius triangularis acutus, duobus parallelis humilibus cristis paucis longis papillis ferens, 1 mm altis. Calcar tumorescens breves haud excavatum farctum, apice rotundo, 1,5–1,8 mm longum, 1–1,3 mm diametro. *Columna* teres, 7 mm longa, 1 mm–

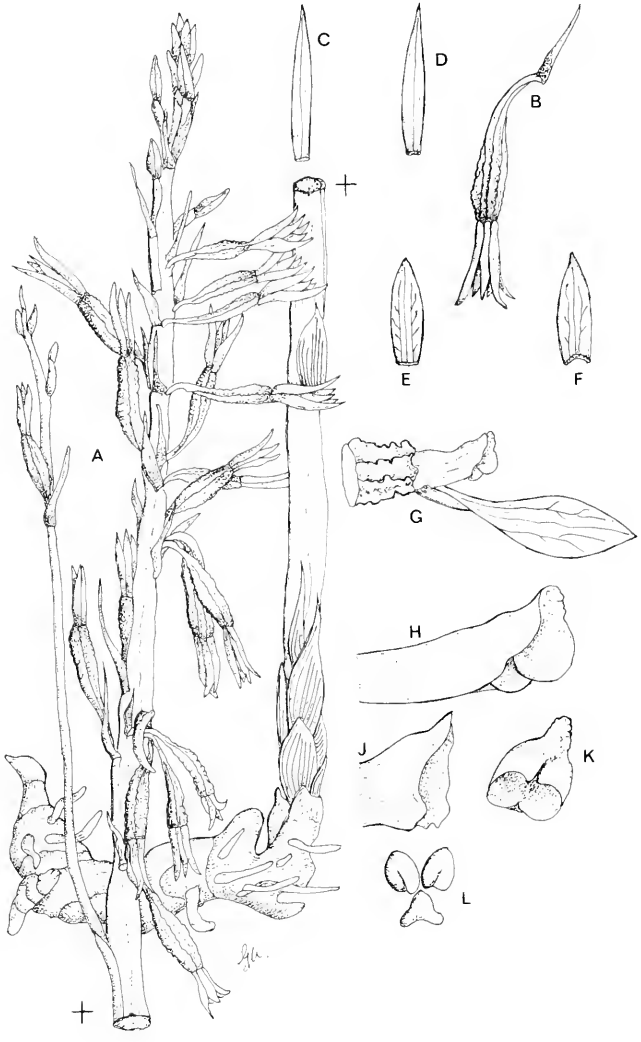

FIG. 5.
Eulophia ecalcarata. A. habit, × $^{2}/_{3}$; B, flower, × 1; C, lateral sepal, × $1^{1}/_{3}$; D, dorsal sepal, × $1^{1}/_{3}$; E, petal, × $1^{1}/_{3}$; F, labellum, × $1^{1}/_{3}$; G, column and labellum, × 3; H, column side view, × 8; J, androclinium, × 10; K, anther cap back view, × 10; L, pollinia, × 10; (all magnifications approximate). All from *G. Williamson 216*.

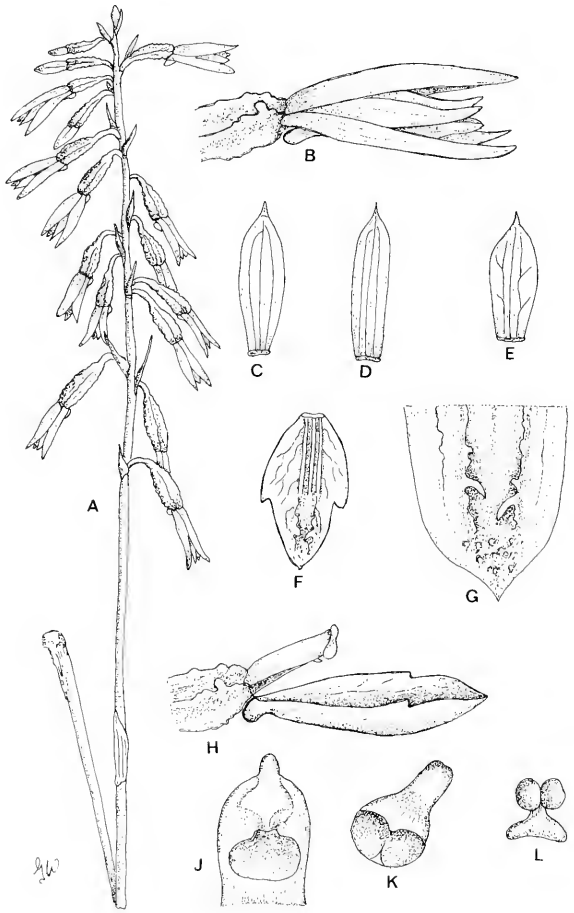

FIG. 6.
Eulophia farcia. A, habit, × $^{2}/_{3}$; B, flower, × 2; C, dorsal sepal, × $1^{1}/_{3}$; D, lateral sepal, × $1^{1}/_{3}$; E, petal, × $1^{1}/_{3}$; F, lip flattened, × $1^{1}/_{3}$; G, epichile, × 8; H, column and labellum, × $2^{1}/_{3}$; J, androclinium from ¾ below, × 10; K, anther cap back view, × 10; L, pollinia, × 12; (all magnifications approximate). All from *G. Williamson and B. K. Simon 1764*.

2 mm diametro, dorsaliter apice prominentia; *stigma* ovalis; *operculum antherae* pyriforme, 2 mm altum; *pollinia* sphaerica, 0,4 mm diametro; *viscidium* triangulare, angulis rotundatis, basi 0,9 mm latum.

Habitat: Open *Brachystegia* woodland.

Critical remarks: When first discovered in 1959 this plant was thought to be a form of *Eulophia nyasae* Rendle. Ten years later a further colony was discovered 80 km to the west of the original colony. The new species differs from *E. nyasae* Rendle in that the lip is boat-shaped with a more acute apex. The lateral lobes are very short. The epichile ornamentation consists of a few papillae as compared with *E. nyasae* Rendle which has a mat of projecting papillae. The plants from the Holmes collection are much more robust than the Williamson collections but agree in every other way. The specific epithet is derived from the existence of a solid spur.

ZAMBIA: West Prov.: In open woodland, Solwezi, Dec. 1959, *W. D. Holmes 0181* (SRGH; K); 80 km W. of Solwezi, growing in heavy red soil in tall wet *Brachystegia* woodland, Dec. 1969, *G. Williamson and B. K. Simon 1764* (SRGH, holotype; K, isotype).

Angraecopsis gassneri Williamson, sp. nov., affinis *A. trifurca* (Rchb.f.) Schltr., folio undulato, operculo antheris apice triangulato acuto, stipitibus verrucosis, viscidiis procurrens ultra rostello differt (Fig. 7).

Typus: Zambia, *G. Williamson and A. Gassner 2448* (SRGH, holotypus; K, isotypus).

Herba epiphytica, glabra, crescens deosum usque 260 mm alta; radices numerosae, implicatae angustae, apicibus expansis, usuqe 120 mm longae, 2 mm diametro, e basi plantae emissae. *Folia* 3–5, disticha, lingulata, leviter undulata, multivenis parallelis, virida fusca nitida 150–220 mm longa, 25–35 mm lata, base 10 mm lata, apice inaequaliter bilobato obtuso. *Pendunculus* 1–5 e basi plantae exortae, teres, usque 160 mm longus, 1 mm diametro, bracteis 4, usque 2 mm longis, 1 mm latis, floribus alternatis fasciculatis terminalibus; *inflorescentia*, usque 4 cm longae, pendulae dense multiflorae. *Flores* usque 20 per inflorescentia, pallidi-virides, bractae lanceolatae, 1 mm longae, acutae; *ovarium* cum *pedicello* valde curvatum, 15 mm longum. *Sepalum intermedium* ovatum, 3 mm longum, 1,8 mm latum, obtusum; *sepala lateralia* lingulata obtusa, apicibus cochlearibus, in centris sepalis retrocurvatis anguli 90°, bases petalis conjuncta, usque 9 mm longa, 1,5 mm lata. *Petala* ovata, in centris longitudinem retroplicatis, 3,5–5 mm longa. 1,5–3 mm lata, leviter acuta. *Labellum* porrectum tripartitum ± 6 mm longum; base indiviso, usque 2 mm longo, lineari, lobo medio lanceolato, 3 mm longo, 0,6–1 mm lato, ± obtuso, lobis lateralibus lanceolatis

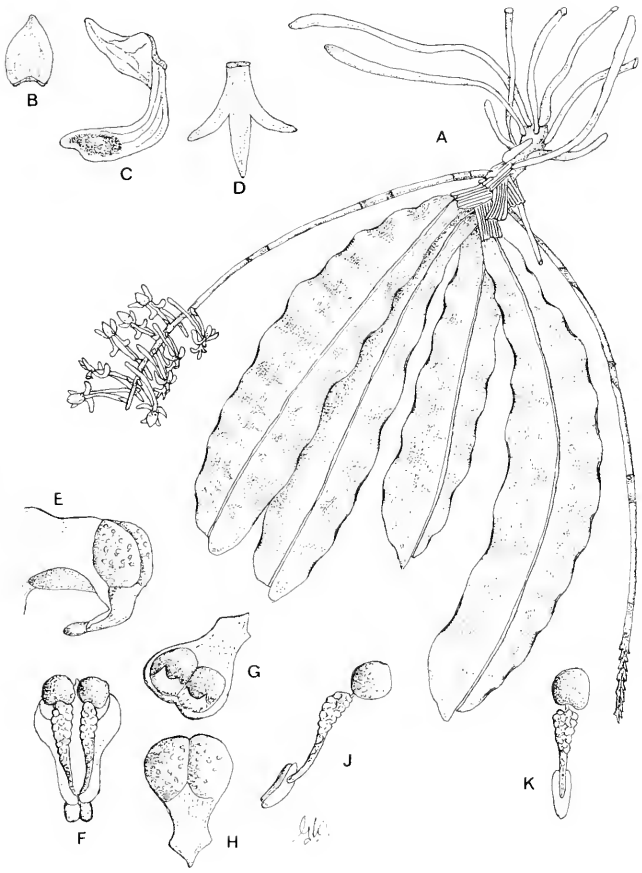

FIG. 7.
Angraecopsis gassneri. A, habit, × ½; B, dorsal sepal, × 5; C, lateral sepal and petal, × 5; D, labellum, × 5; E, column, × 20; F, apex of column with pollinia in position, × 20; G, anther cap back view, × 20; H, anther cap front view, × 20; J, pollinium, stipes and viscidium side view, × 20; K, pollinium, stipes and viscidium front view, × 20; (all magnifications approximate). All from *G. Williamson and A. Gassner 2448*.

curvatis extrinsicus, 2,8 mm longis, 0,4–0,7 mm latis, ± obtusis; *calcar* cylindratum, curvo parallele ad ovarium, 15–18 mm longum, 0,8–1 mm diametro. *Columna* ± teres, 1–1,8 mm longum; *stigma* fere reniforme, 1 mm latum; *operculum antherae* pyriforme, basis leviter papillosum, usque 1 mm longum, apex curvatus triangulatus acutus; *pollinia* 2, sphaerica; *stipites* clavati valde verrucosi, 0,8 mm longa; *viscidia* angusta elliptica, 0,4 mm longa; *rostellum* tripartitum productum, lobis apicibus obtusis, recurvatum versus stigma, 0,4 mm longum; *viscidiis* procurrens utra rostello apice.

Critical remarks: *Angraecopsis gassneri* is closely related to *A. trifurca* (Rchb.f.) Schltr. with which it has been previously confused. The new taxon has distinctive undulating to corrugated leaves. Unlike *A. trifurca* (Rchb.f.) Schltr. the anther cap has a drawn-out apex which is three-cornered and acute. The stipites are clavate and quite clearly verrucose whereas in *A. trifurca* (Rchb.f.) Schltr. the stipites are linear entire. The viscidia in *A. gassneri* project well beyond the rostellum lobe apices whereas in *A. trifurca* (Rchb.f.) Schltr. they tend to be hidden. This new species is named in honour of Mr A. Gassner who was the co-collector and flowered the type specimen in Lusaka, Zambia.

ZAMBIA: Western Prov.: Zambesi Rapids near Kalene Hill, Mwinilunga District, col. Oct. 1965, fl. Lusaka March 1966, *G. Williamson 149* (K); Mwinilunga Distr. *W. D. Holmes 0349* (K, SRGH); in centre of rain forest on islands in Zambesi River near Kalene Hill, col. Feb. 1975 fl. Lusaka April 1975, *G. Williamson and A. Gassner 2448* (SRGH, holotype; K, isotype).

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The author is indebted to the directors and curators of the following herbaria: Royal Botanic Gardens, Kew; Bolus Herbarium, University of Cape Town and National Herbarium of Rhodesia, Salisbury.

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Jl S. Afr. Bot. 46 (4): 343–354 (1980)

PERIODICITY IN FYNBOS OF THE NON-SEASONAL RAINFALL BELT

W. J. Bond

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Abstract

Shoot elongation, flowering and leaf fall were recorded for one representative each of the proteoid, ericoid and restioid life form of fynbos on the Outeniqua mountains near George and the lower slopes of the Swartberg, Swartberg Pass. Maximum growth for restios was in winter/spring, for proteoid species summer, whilst ericoid species grew all the year round. Maximum leaf fall for all life forms was in late summer in the Outeniquas and autumn in the Swartberg. Flowering season varied between and within life forms. Results are discussed in relation to seasonality in Californian chaparral and Australian heathland.

Uittreksel

PERIODISITEIT IN FYNBOS VANAF DIE NIE-SEISOENALE REËNSTREEK

Lootverlenging, blomtyd en blaarval is aangeteken vir een verteenwoordiger van elk van die proteoid, ericoid en restioid groeivorms van fynbos op die Outeniekwaberge naby George en laer hange van die Swartberg, Swartbergpas. Maksimum groei vir restios was gedurende winter/lente, vir proteoid species gedurende die somer, terwyl ericoid species deur die hele jaar gegroei het. Maksimum blaarval het gedurende laat somer in die Outeniekwas en herfs in die Swartberg vir alle groeivorms voorgekom. Blomseisoen het tussen en binne groeivorms gevarieer. Die resultate word bespreek in verhouding tot seisoenaliteit in Kaliforniese „chaparral" en Australiese „heathland".

Introduction

The diversity of plant life in any one locality is dependent on the degree to which resources are partitioned between competing populations. Temporal partitioning of resources is one aspect of niche differentiation in plant communities. Seasonality in the species rich Cape fynbos has been recorded by Kruger (1980) and Williams (1972) who noted varied phenorhythms in different life forms and within life forms.

Seasonality is not only of interest in exploring modes of competition, but also the interrelationships of plants and consumers—especially nectarivores, and the response to different fire regimes and fire seasons. Very little is known about the influence of seasonal events in fynbos on consumers. In the Swartberg, for example, nectarivores appear to be dependent on *Protea eximia* when other Proteaceae are not flowering. This species flowers throughout the year with apparent peak flowering in summer whereas most other Proteas flower from late summer to early winter. Management affecting the species would thus affect a

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number of dependent organisms. Optimal fire season is also linked to phenology since post-fire survival is partly dependent on flowering and fruiting periodicity, particularly for species with short-lived seeds lacking in fire protective devices. Jordaan (1949, 1965) observed poor regeneration of *Protea repens* (= *mellifera*) in winter burns which he ascribed to the phenological status at the time of burn. He divided fire seasons into safe, unfavourable and dangerous according to phenophase.

This note reports one year's observation on seasonal rhythms of the proteoid, ericoid and restioid life forms in the non-seasonal rainfall zone of the Outeniqua (coastal) and Swartberg (inland) mountains of the Southern Cape. It is hoped that despite the study's limitations it may stimulate greater interest in a rich and poorly explored field where the ecophysiologist, in particular, has much to offer.

Study Area

Plants were studied from two localities. These were Tierkop (S 33 ° 55′ E 22 ° 31′) a hill on the Outeniquas behind Saasveld Research Station, near George, and Swartberg Pass (S 33 ° 22′ E 22 ° 6′) on the Great Swartberg Range. The Tierkop site was at an elevation of 520 m on a E.S.E. aspect of 20% slope. The soil was a dark, acid, loamy lithosol (Mispah Form) with a relatively high organic matter content, derived from Table Mountain Sandstone. The Swartberg study area was located near the southern foot of the pass at 950 m on a southern aspect of 25% slope. The soil was litholic (Glenrosa Form) and with a moderately deep, neutral, coarse sandy loam topsoil overlying a shallow subsoil which overlies Table Mountain Sandstone.

Climate

Outeniquas: The Tierkop site on the Outeniquas has a mild temperate climate, classified as Cfb in the Köppen System (Köppen, 1931). Mean monthly temperature and rainfall at George (Weather Bureau, 1960) about 5 km from the site is summarised as a climate diagram (Walter and Lieth, 1967) in Figure 1. Mean annual temperature is 16,4 °C and precipitation is 850 mm of which 42% falls in the winter half year. Potential evapotranspiration (P.E.T.), defined as "the water loss which will occur if at no time there is a deficiency of water in the soil for use of vegetation" (Thornthwaite, 1944), has been calculated for George using Penman's formula (ex Israelsen & Hansen, 1966). (Fig. 1). A deficit between rainfall and P.E.T. is apparent over the summer months and a moisture excess in winter. The effective moisture regime thus resembles a winter rather than a summer rainfall region. This is confirmed by streamflow records for the Kaaiman's River, the drainage of the Tierkop catchment, which has minimum runoff in December, January and February (Department of Water Affairs, unpublished records, 1960 to 1970).

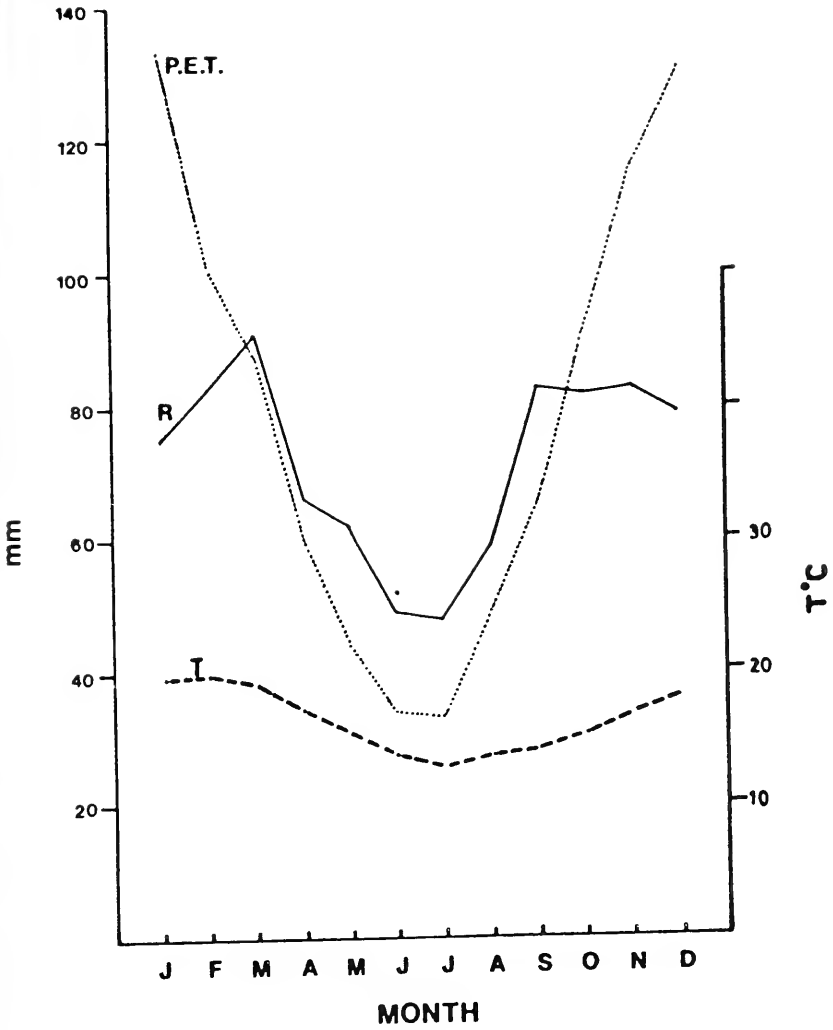


FIG. 1.
Climate diagram (Walter & Lieth, 1967), George (S 33 ° 58′, E 22 ° 25′, elevation 221 m) 1878–1950 with Penman estimates of Potential Evapotranspiration (P.E.T.).

Swartberg: The Swartberg area has a "steppe" type climate classified as BSk in the Köppen system. Climatic data from the Cango Caves station, situated about 12 km from the Swartberg site and in a similar position, are summarised in Figure 2. Mean annual temperature is 16,5 °C and precipitation (1955–1970) is 363,1 mm of which 49% is winter rainfall (Weather Bureau, unpublished records). Inadequate data prevented calculation of P.E.T., but a similar pattern to Tierkop with maximum moisture stress in the summer months is probable. This is indirectly confirmed by Perdepoortrivier streamflow records (1965–1976) from a catchment on the southern slopes between Swartberg Pass and Cango Caves. Minimum runoff is between December and March and maximum between April and September (Department of Water Affairs, unpublished records).

Deviations from mean monthly values of rainfall and temperature of George and Cango Caves during the study period are listed in Table 1 (Weather Bureau, unpublished).

Vegetation

Tierkop, Outeniquas

The Tierkop site was situated on a broad interfluve on the Outeniqua mountains. The vegetation was a mature 1,5–2 m high proteoid shrubland dominated by *Leucadendron uliginosum* R. Br. subsp. *uliginosum* in the upper stratum. Mid-layer shrubs were mostly *Erica seriphiifolia* Salisb. with associated *Penaea cneorum* E. Mey. A relatively dense layer of Cyperaceae (mainly *Tetraria*

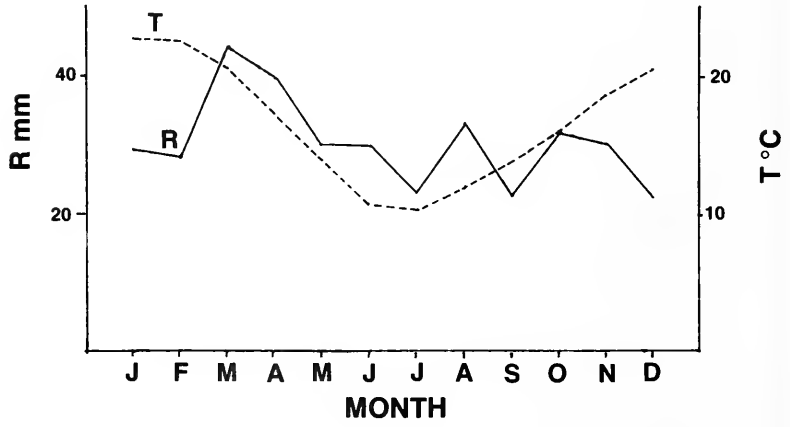


Fig. 2.
Climate diagram, Cango Caves (S 33 ° 23′, E 22 ° 13′, elevation 640 m), 1955–1970.

TABLE 1

Percentage deviation from monthly values of mean rainfall and temperature for George and Cango Caves over the study period, 1977–1978

Year		1978					1977								
Month		J	F	M	A	M	A	M	J	J	A	S	O	N	D
Rainfall Deviation	George	−2,8	−71,0	−37,9	−28,8		−58,6	+164,4	−56,5	−72,3	+78,8	+48,3	−41,6	+26,1	−31,1
	Cango Caves	+112,3	−78,7	−84,1	−60,8	−25,0			+77,4	−26,4	+14,3	+87,2	−0,6	+40,5	+38,4
Temperature Deviation	George	+5,4	−2,0	+7,0	+1,2		+10,8	−1,4	+5,0	+15,7	+11,8	−3,5	+7,8	+7,0	+8,6
	Cango Caves	+4,6	+2,8	−7,7	+11,7	+3,0			−5,3	−4,6	+0,9	+3,7	0,0	−0,5	−3,3

capillacea (Thunb.) C. B. Cl.) and Restionaceae (*Elegia parviflora* Kunth, *Restio triticeus* Rottb., *R. compressus* Rottb. and *E. juncea* L.) was present. The community is widespread on warmer, mid and upper elevation slopes in the Outeniqua and Tsitsikamma mountains.

Swartberg Pass

The study area was on the lower foothills, near the transition to Mountain Rhenosterveld on Nama System shales. The vegetation was a mature, 1,5 to 2,0 m proteoid shrubland dominated by *Protea repens* (L.) L. in the upper stratum associated with *P. eximia* (Knight) Fourc. *Phylica paniculata* Willd. was common in a species rich shrub layer with associated *Protea lorifolia* (Knight) Fourc., *Agathosma mundii* Cham and Schlechtend, *Stoebe* spp., *Anthospermum*, etc. Large restio tussocks occurred with frequent *Restio fruticosus* Thunb., *Cannamois dregei* Pillans, *Willdenowia teres* Thunb. and *Hypodiscus striatus* (Kunth.) Mast. Sedges and grasses, about equally represented, were of minor significance. The community is representative of relatively xeric southern slope vegetation on the Swartberg.

Methods

Species belonging to three representative life-forms were selected at each site. These were *Leucadendron uliginosum* ssp. *uliginosum* (proteoid), *Erica seriphiifolia* (narrow-leaved, ericoid shrub), and *Elegia parviflora* (restioid) on Tierkop and *Protea repens* (proteoid), *Phylica paniculata* (narrow-leaved, ericoid shrub) and *Restio fruticosus* (restioid) at Swartberg Pass.

Four plants each of the Proteaceae and Restionaceae and three each of the ericoid shrubs were selected. Four stems on each of the shrubs were marked and four young *Restio* shoots on each restio.

Shoot elongation was measured monthly between April 1977 and April 1978 at Tierkop and June 1977 to May 1978 in the Swartberg. Bud set or development, flowering, fruiting and leaf colouring or fall were recorded for each individual, and flowering periods for other, unmarked species recorded simultaneously.

Results

Growth is defined here as shoot elongation and/or leaf expansion. Seasonal growth patterns of different life forms were compared by plotting mean percentage increment over the previous months shoot length (Fig. 3a and b). Growth seasons within similar life forms were strikingly similar in the two localities despite the use of different species. The proteoid species grew over the dry summer months in both areas. *Leucadendron uliginosum* commenced growth in early October, peaked in the dry month of February and ceased in April, slightly earlier than the summer-autumn growth season for Leucadendrons recorded elsewhere (Williams, 1972; Kruger, 1980). The growth patterns of *Protea repens* resembled Kruger's

(1980) observations, but events were out of phase by two or three weeks. New shoot growth was initiated in September and October, with maximum shoot elongation between mid-November and early December. A second flush of growth was evident, peaking early in March. Differences in growth season between *Protea* and *Leucadendron/Leucospermum* noted by Kruger were not apparent but more information is required on a wider variety of species.

Kruger (1980) records a late winter to early spring growth season for most fynbos shrubs. The ericoid species had no specific growth season though growth ceased or was slowest in the autumn months of April and May in the Swartberg and was least from January to May in the Outeniquas.

The restioid life forms had a well-defined growth season from late autumn to late spring (November) with some growth until February in both. This is earlier than Kruger's 1978 generalisation of a spring to early summer growth season for winter rainfall Restionaceae.

Flowering

Periods of budset and development and flowering are indicated in Figure 3. The Outeniqua species flowered from spring to mid-summer. *Leucadendron uliginosum* flowered from October to early in December. This is later than most Leucadendrons of the winter rainfall area (Williams, 1972). Plant species were recorded flowering at all times of the year within the vicinity of the plot with the least flowering in autumn and early winter.

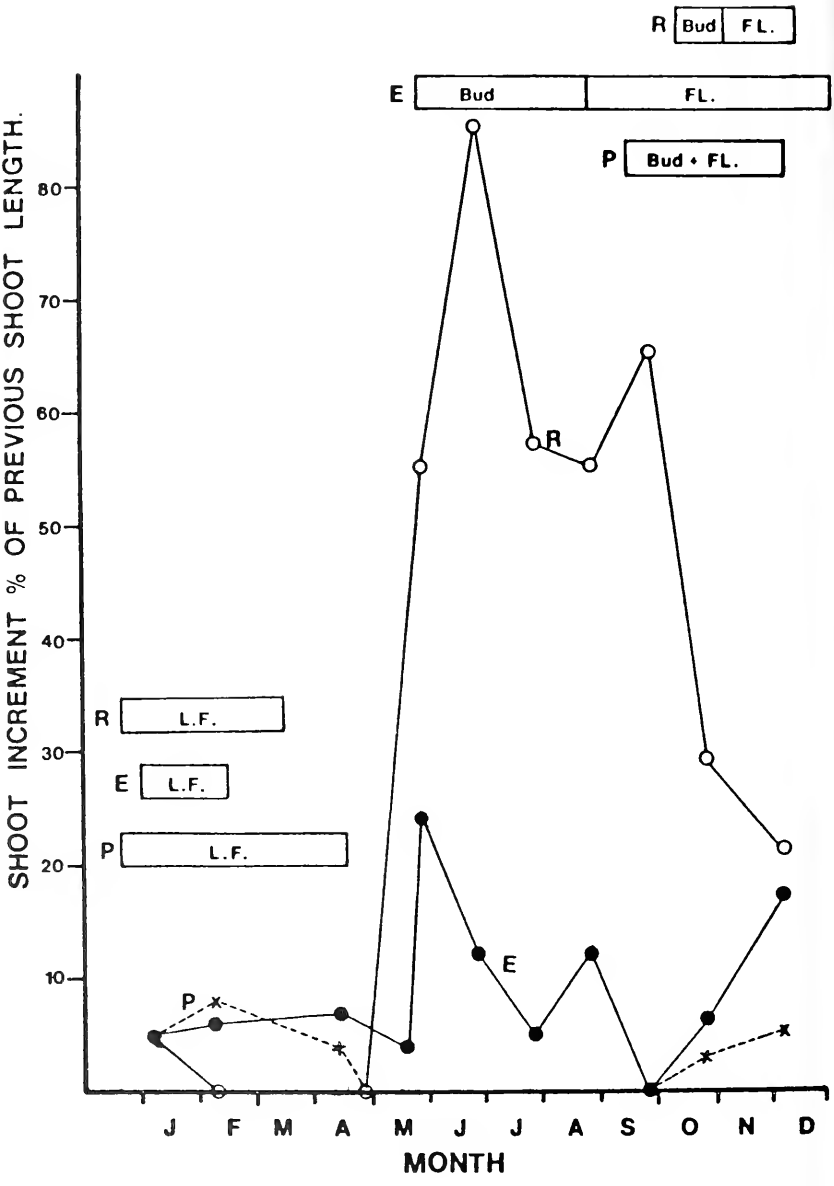
Flowering periods for the Swartberg are indicated in Figure 3b. *Protea repens* flowered from the end of February to mid-May with peak flowering in March/April. This is appreciably earlier than the May to July period (Burger, 1973 in Kruger, 1980) for *P. repens* in the Western Cape. Both the restioid *(R. fruticosus)* and ericoid *(Phylica paniculata)* growth forms flowered about two months later than their analogues on the Outeniquas, but, as in the Outeniquas, some species in the vicinity were present in flower throughout the year.

Leaf-Fall

Period of leaf-fall or partial stem die-back (in the case of Restionaceae) are indicated in Figure 3. Leaf-fall was comparatively synchronised for all the life forms studied. Kruger (1980) reported a principal leaf-fall period in late summer to autumn for Western Cape species to which the Swartberg data conforms. In the Outeniquas, however, leaf-fall was earlier being mainly mid- to late-summer.

Discussion

This report describes observations over a limited period and for a limited number of species. More extended observations over a greater geographical range are required, together with studies of the relationship between stem elongation and


R Bud FL.
E Bud FL.
P Bud + FL.
SHOOT INCREMENT % OF PREVIOUS SHOOT LENGTH.
80
70
60
50
40
30
20
10
R
E
P
R L.F.
E L.F.
P L.F.
J F M A M J J A S O N D
MONTH

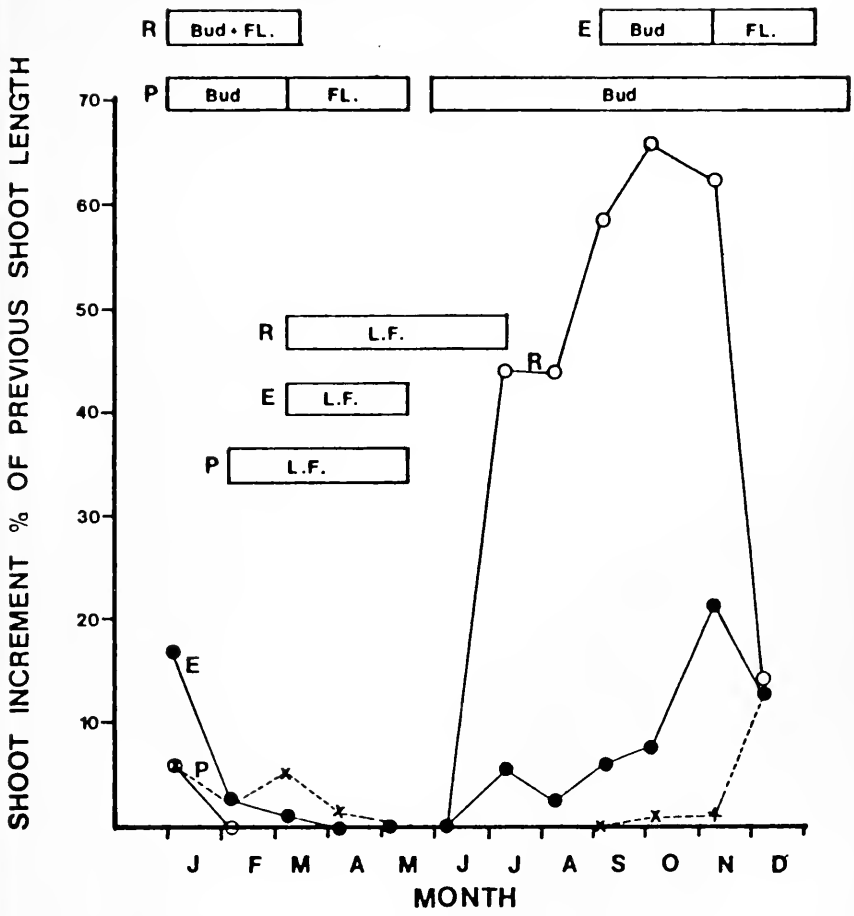


FIG. 3.
Shoot elongation as mean percentage increment over shoot length at the preceding measurement. Measurement intervals were approximately one month. Life forms and species are, for (a) R = *Elegia parviflora*, E = *Erica seriphiifolia*, P = *Leucadendron uliginosum*, and for (b) R = *Restio fruticosus*, E = *Phylica paniculata*, P = *Protea repens*. Periods of bud development (BUD), flowering (FL) and leaf-fall (L.F.) are indicated for each species. 3(a) Outeniquas, 3(b) Swartberg.

carbon gain and water loss. Nevertheless some interesting points arise. Growth periodicities are adaptations to seasonal stress on plant growth. Probable seasonal limitations on plant growth in the study area are:

Winter: Light (short photoperiod), low temperature. Water supply is more than sufficient.

Spring: Light is adequate (medium length photoperiod), temperatures are moderate, water supply is adequate. Apparently optimum conditions for growth.

Summer: Long photoperiods and warm temperatures are suitable for growth. Soil moisture deficit strongly limiting particularly as season progresses.

Autumn: Similar to spring but with a marked soil moisture deficit initially and gradual recharge towards winter.

It seems probable that nutrient availability will vary with season due to seasonal variations in litterfall and the effects of climate on decomposition (Schaefer, 1973) and that this may also affect growth periodicity. This sequence is characteristic of ecosystems with a Mediterranean climate. In California, *Heteromeles arbutifolia*, a sclerophyll shrub, is strongly limited by moisture in summer, with short photoperiod limiting in winter and temperature of minor significance in seasonal control of carbon gain (Mooney & Harrison, 1975). The dominant life form (in Californian chaparral), an ever-green sclerophyll, deep-rooted shrub, is adapted to carbon gain whenever favourable conditions of light, moisture or temperature coincide. It tolerates drought and cool winter temperatures (Morrow & Mooney, 1974). Growth periodicity tends to be bimodal with spring as the main growth season. Seasonal growth in the more humid communities of Australian sclerophyll, is confined to spring and summer. This is out of phase with the climate and has led to the suggestion of a tropical origin of the flora and its comparatively recent confinement to a Mediterranean climate (Specht, 1975).

The Cape fynbos seems to be unique for its variety of different life forms and for the range of growth periodicities adopted.

The Restionaceae in this study are unusual in opting for a growth period commencing in early winter in low temperature–low light conditions. By spring, when optimal conditions prevail, young shoots are well established and vigorous. Winter drought towards the summer rainfall areas would severely limit the distribution of these species and reduce their competitive advantage.

The two ericoid shrubs (particularly *Erica seriphiifolia*) have adopted a generalist strategy (cf. Morrow & Mooney, 1974) growing at any period when the combination of soil moisture, temperature and photoperiod is suitable. They thus resemble chaparral shrubs in growth periodicity. *Phylica paniculata*, in the Swartberg, showed a distinct peak in spring to mid-summer with limited growth in

winter or autumn perhaps as a consequence of greater moisture and temperature stress in the drier climate and colder winters.

The Proteaceae grow in the driest period of the year, resembling dominant shrubs in Australian heath and mallee (Specht and Brouwer, 1975). This summer growth season would be better suited to summer rainfall areas and adds weight to the argument of a tropical or sub-tropical origin for the family (Rourke, 1972, for *Leucospermum*; Johnson & Briggs, 1975).

Phenology is probably implicated in community diversity. From the limited evidence available, the specialised summer growth strategy appears to have few adherents and the difficulties of growth in the season of maximum moisture stress is perhaps reflected in the low number of species in any community occupying the proteoid niche. In contrast the all year growth capabilities of ericoid and narrow sclerophyll shrubs would seem sufficiently flexible to allow subtle seasonal division of resources between species and thus a large number of species within the life form. Comparative studies of species within a life form, and the relative proportion of life forms with different growth periodicities along moisture/temperature/photoperiod gradients would provide further clues to the role of phenology in allowing many species to grow together in a structurally simple vegetation type.

Acknowledgements

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KARYOTYPE ANALYSIS OF THE GENUS *EUCOMIS* (LILIACEAE)

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Abstract

Ten *Eucomis* spp. were investigated cytogenetically. Diploids ($2n = 30 = 2x$) and tetraploids ($2n = 60 = 4x$) occur in the genus and each karyotype consists of macro- and microchromosomes.

Uittreksel

KARIOTIPE ANALISE VAN DIE GENUS *EUCOMIS* (LILIACEAE)

Uit 'n sitologiese ondersoek wat op tien *Eucomis* spesies gedoen is, is diploïede ($2n = 30 = 2x$) en tetraploïede ($2n = 60 = 4x$) gevind en elkeen se kariotipe bestaan uit makro- en mikrochromosome.

1. Introduction

The genus *Eucomis* L'Hérit. or pineapple lilies are represented in Southern Africa by ten species, of which five are endemic to the Republic of South Africa.

Since Reyneke (1972) found difficulty in distinguishing morphologically between certain species and subspecies of the genus, chromosome counts were made. From these counts it became clear that karyotype studies would provide a considerable amount of additional information that could be used in an attempt to elucidate the phylogeny of the genus.

2. Material and Method of Investigation

Bulbs of different *Eucomis* plants were placed on moist vermiculite at the beginning of a growing season. Young roots which were approximately 10 mm long, were collected between 11h30 and 12h30 and treated in a 0,05 % colchicine solution for 1½ hours. This material was then fixed in Pienaar's fixative (Pienaar, 1955). Good results were also obtained with pre-fixation treatment of three hours in a saturated solution of paradichlorobenzene followed by fixation in either Pienaar's fixative or Carnoy's fixative (Haskell & Wells, 1968). After a fixation period of 24 hours at room temperature, the material was transferred to 70% ethanol and stored at 0–5 °C.

Prior to staining with leucobasic fuchsin for 1–1½ hours (Haskell & Wells, 1968) the material was hydrolised for 12–14 minutes in 1M HCl at 60 °C. After

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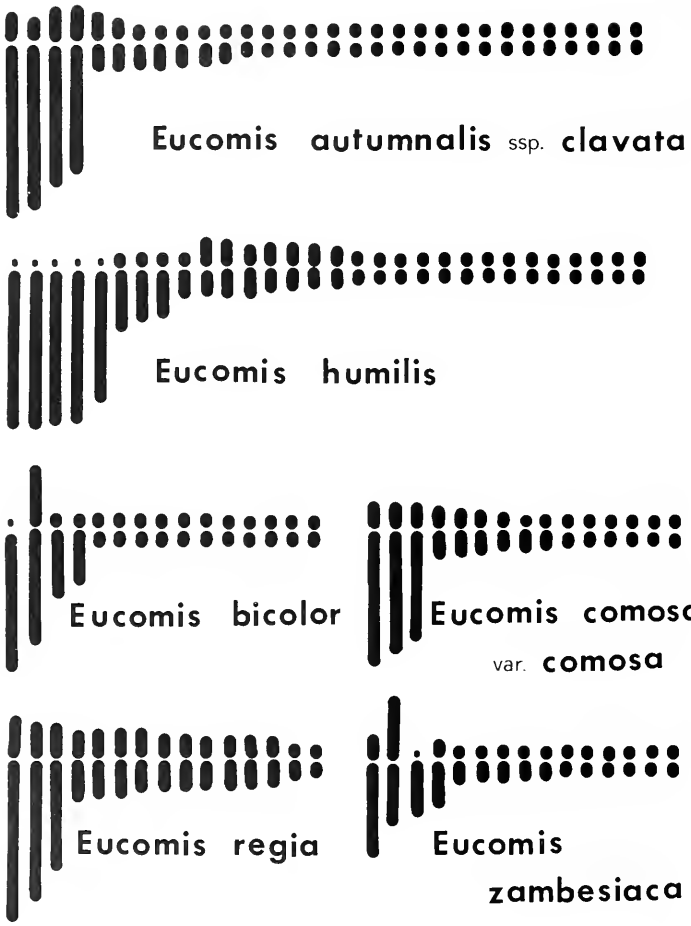
Eucomis autumnalis ssp. clavata
Eucomis humilis
Eucomis bicolor
Eucomis comosa
var. comosa
Eucomis regia
Eucomis
zambesiaca

staining, the material was rinsed in tap water for 1–3 minutes, squashed between a microscope slide and a cover slip, dehydrated in an alcohol series and mounted in euparal.

Chromosome studies of *E. comosa*, *E. montana*, *E. schijffii* and *E. zambesiaca* were limited to one or two plants only due to the unavailability of more material while in all other species at least five specimens from different localities were studied.

3. Results and Discussion

3.1 *Chromosome morphology*

Macro- and microchromosomes (Fig. 1) were present in the karyotype of all *Eucomis* spp.

Due to variation in the microchromosome number of certain species (see Table 1) it was therefore decided to restrict the identification of a karyotype mainly to the number of macrochromosomes. In some species however, e.g. *E. humilis*, intermediate chromosome sizes occur preventing precise classification of chromosomes.

In all the *Eucomis* species examined the macrochromosomes are submetacentric or acrocentric and there is a marked difference in size of a given karyotype. According to the definition of Stebbins (1971) an asymmetric or advanced karyotype has acrocentric chromosomes and the largest and smallest chromosomes differ conspicuously. The karyotype of the genus *Eucomis* is therefore advanced as far as chromosome morphology is concerned.

The most advanced karyotype apparently is that of *E. comosa* var. *comosa* (Fig. 1) where six clearly distinguishable macrochromosomes and 24 microchromosomes are present. This distinction is not as conspicuous in *E. regia*.

E. regia and *E. schijffii*, which are morphologically very similar, can easily be distinguished cytologically since *E. regia* has 6 macro- and 24 microchromosomes while *E. schijffii*, like *E. zambesiaca*, has 8 macro- (4 long, 4 medium) and 22 microchromosomes.

E. humilis ($2n = 60$) has the most primitive karyotype of the polyploid *Eucomis* species, and *E. regia* ($2n = 30$) the most primitive of the diploid species because their chromosomes exhibit continuous variation from the macro to the micro form. The three remaining diploid species, viz. *E. vandermerwei*, *E. zambesiaca* (Fig. 1) and *E. schijffii*, each with 8 macro- (4 long, 4 medium) and 22 microchromosomes represent an intermediate group between the advanced *E. comosa* var. *comosa* and the primitive *E. regia*.

3.2 *Changes in ploidy*

In the genus *Eucomis* diploids and tetraploids were found. The number of chromosomes in all the diploids is 30 ($2n = 30 = 2x$) while polyploids have 60

TABLE 1.

Chromosome numbers and the number of macrochromosomes in different species, subspecies and varieties of the genus *Eucomis* L'Hérit.

Species	Localities	No. of Macro-chromo-somes	Diploid number	Author
E. autumnalis (Mill.) Chitt. subsp. *autumnalis*	Hogsback	8	60	Koerperich (1930) Riley (1962) Reyneke
E. autumnalis subsp. *amaryllidofolia* (Bak.) Reyneke	Fauresmith	8	60	Reyneke
E. autumnalis subsp. *clavata* (Bak.) Reyneke	Pretoria	8 8	30 60 60–64	De Wet (1957) Riley(1962) Reyneke
E. bicolor Bak.	Cathedral Peak	4	30–32 (34?) 32	Müller (1912) Darlington (1926)
		8	30	Matsuura & Sutô (1935)
		4	30–32	Reyneke
E. comosa (Houtt.) Wehrh. var. *comosa*	Cultivated	6	60	Matsuura & Sutô (1935)
		8	60	Sâto (1941)
		6	30	Reyneke
E. comosa var. *striata* (Donn) Willd.	Ixopo	10	60	Reyneke
E. humilis Bak.	Cathedral Peak	10	60	Reyneke
E. montana Compton	Belfast	8	60	Reyneke
E. pallidiflora Bak. var. *pallidiflora*	Port Shepstone	8	60	Reyneke
E. pallidiflora var. *poleevansii* (N. E. Brown) Reyneke	Belfast	8	50 60–64	De Wet (1957) Reyneke
E. regia (l.) L'Hérit. subsp. *regia*	Napier	6	30	Reyneke
E. regia subsp. *pillansii* (L. Guthrie) Reyneke	Kamieskroon	6	30	Reyneke
E. schijffii Reyneke	Cathedral Peak	4	30–32	Reyneke
E. vandermerwei Verdoorn	Middelburg	4 4	20 30	De Wet (1957) Reyneke
E. zambesiaca Bak.	Blouberg (Pietersburg)	4	30–32	Reyneke

chromosomes ($2n = 60 = 4x$). Except for the results obtained by De Wet (1957) this corresponds with results of most previous authors (see Table 1) even in respect of the number of macrochromosomes. De Wet's results are dubious because he used microtome sections for counting chromosomes.

A chromosome count of a cultivated plant of *E. comosa* var. *comosa* from an unknown original locality gave $2n = 30$. This differs from published counts (Matsuura & Sutô, 1935; Sâto, 1941) but var. *striata* may possibly have been examined by these authors, accounting for this discrepancy.

Except for *E. humilis* which produces a relatively small number of seeds, all the *Eucomis* spp. are fully fertile. It is therefore probable that the fertile polyploids are allotetraploids and *E. humilis* is a autotetraploid or even more a segmental allotetraploid. In general the karyotypes are in agreement with these suggestions since none of the tetraploids have chromosomes that occur in sets of 4. At best the macrochromosomes could be grouped in pairs only. This would suggest a hybrid polyploid origin in which the hybridisation occurred between diploids with divergent karyotypes.

The popular conception that polyploids are larger plants than their diploid relatives holds true in the genus *Eucomis*. Eight of the fifteen *Eucomis* taxa are tetraploids and the plants of all these taxa are larger than the seven diploid taxa.

Another result of the duplication of chromosomes is the fact that the tetraploids were observed to grow more slowly than their diploid relatives resulting in a relatively late and lengthy flowering period.

4. Acknowledgements

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A FLUORESCENCE TECHNIQUE FOR THE DETECTION OF KNOBS IN THE MITOTIC CHROMOSOMES OF MAIZE

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Abstract

A fluorescence technique is described for the detection of knobs in the mitotic chromosomes of maize. The method possesses several advantages over conventional techniques based on pachytene analysis.

Uittreksel

'N FLUORESSENSIE TEGNIEK VIR DIE OPSPORING VAN KNOPPE IN DIE MITOTIESE CHROMOSOME VAN MIELIES

'n Fluoressensie tegniek vir die opsporing van knoppe in die mitotiese chromosome van mielies word beskryf. Die metode het sekere voordele bo ander konvensionele tegnieke wat op pagiteen analise gebaseer is.

Introduction

Conventional techniques for the identification of maize chromosomes have relied to a great extent on the recognition of "chromosome knobs", these being condensed regions of chromosome visible most readily during the pachytene stage of meiosis in the pollen mother cells. However, Vosa and De Aguiar (1972) demonstrated that the positions of the knobs may also be recognised as bands in mitotic chromosomes treated by the Giemsa staining technique of Vosa and Marchi (1972).

The present work describes a fluorescence technique, by means of which the positions of the knobs in mitotic chromosomes may be recognised with even greater clarity. Like the Giemsa technique, the method is a c-banding technique for heterochromatin, based on an initial denaturation-reannealing. However, this is succeeded in the present case not by Giemsa staining, but by treatment with a fluorochrome, namely the AT-binding, bibenzimidazole derivative "Hoechst 33258".

Material and Methods

Actively growing root tips of the South African maize cultivar "Early Pearl" were pre-treated by immersion in saturated, aqueous α-monobromonapthalene for 4–5 hours, rinsed in deionised water, and fixed in 3:1 ethanol:glacial acetic acid

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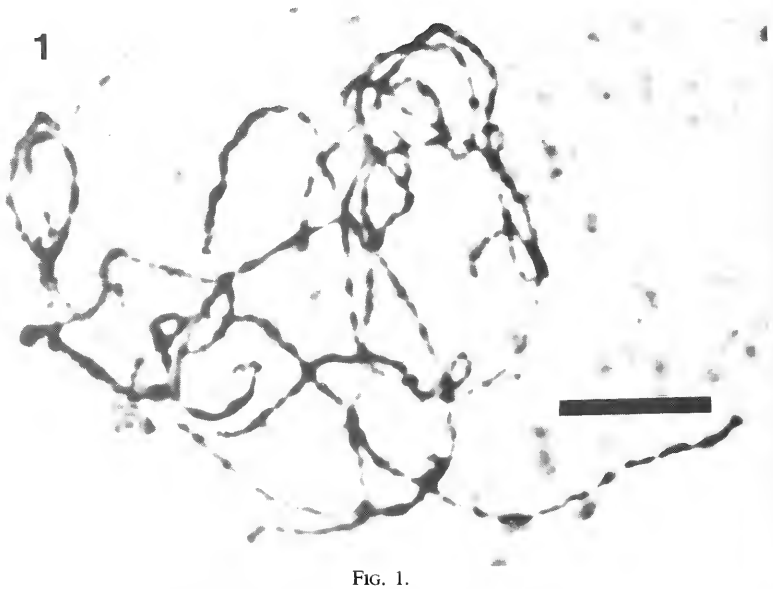

FIG. 1.
Chromosome Knobs in *Zea mays* Var. "Early Pearl".
Pachytene stage in pollen mother cell. Feulgen/Acetic orcein staining, phase contrast.

Bars represent 10 μ

for 8–24 hours. They were then hydrolysed in 0,2N HCl at 60 °C for 2½ minutes, and squashed in 45 % acetic acid under an albumenised coverslip, the latter being floated off in absolute alcohol and air-dried. At this stage the preparations could be stored indefinitely at room temperature without appreciable deterioration.

Following this, the coverslips were immersed for 6 minutes in a saturated, aqueous solution of barium hydroxide at room temperature, rinsed in running deionised water, incubated in 2 X saline sodium citrate buffer at 60 °C for one hour, rinsed again in deionised water, and air-dried. The preparations were then stained for 5 minutes in a 0,02 % ethanolic solution of Hoechst 33258, rinsed in ethanol, air-dried, mounted in 50 % glycerol, and viewed using a Zeiss fluorescence microscope with exciter filter BG12 and barrier filters 50 plus 53. Photographs were taken using Kodak Tri-X Pan film.

If desired, the preparations could then be made permanent by Giemsa staining according to the method of Vosa and Marchi (1972). The procedure in this case was for the coverslips to be floated off in deionised water, stained for 1 hour in a 0,5 % solution of Giemsa buffered to pH 6,8, air-dried and mounted in Gurr's Depex.

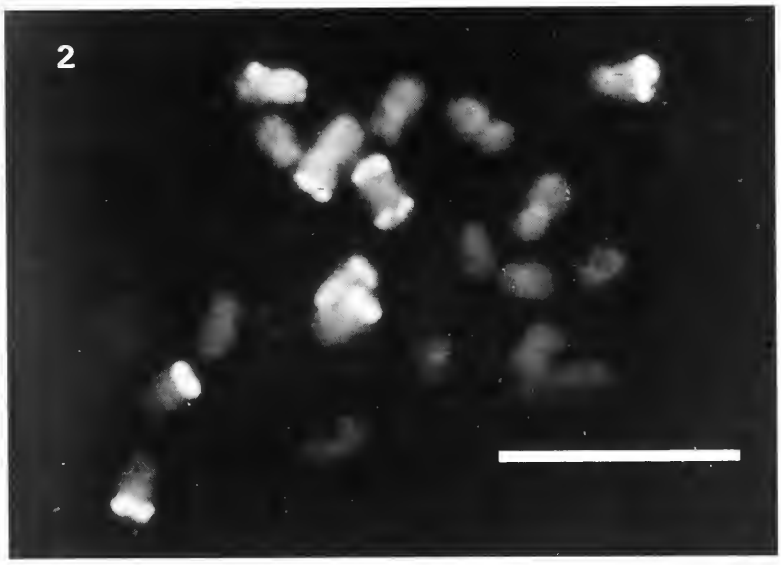

FIG. 2.
Chromosome Knobs in *Zea mays* Var. "Early Pearl".
Root tip metaphase, stained by fluorescence technique described in text.

Bars represent 10 μ.

RESULTS AND DISCUSSION

The knob regions are revealed by the fluorescence technique as bands of intense fluorescence (Fig. 2), and correspond to those regions staining heavily with Giemsa (Fig. 3). Both the fluorescence and the Giemsa methods yield good results, though for the most part the fluorescence technique is the more consistent, being less sensitive to minor variations in the temperature of denaturation and the duration of staining.

Both methods possess many advantages over conventional techniques based on pachytene analysis. The latter frequently necessitate waiting considerable periods of time for meiotic material to become available, and resolution of the pachytene chromosomes themselves may be difficult due to their length, entanglement, and fusion of the knob regions. The degree of clumping of the chromosomes at pachytene is in fact itself under genetic control (Wellwood and Randolph, 1957).

In contrast, the fluorescence and Giemsa techniques, being based on mitotic chromosomes, remove almost all the above difficulties and greatly facilitate karyotype analysis.

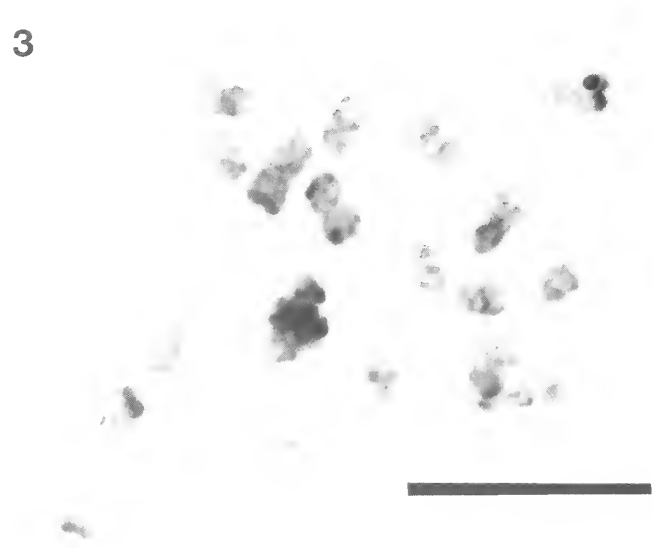

FIG. 3.
Chromosome Knobs in *Zea mays* Var. "Early Pearl".
The same cell as in Figure 2, stained by the Giemsa technique of Vosa and Marchi (1972).

Bars represent 10 μ.

ACKNOWLEDGEMENT

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STUDIES IN THE GENUS *WATSONIA* MILLER

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Abstract

The *Watsonia meriana* (L.) Miller complex is studied and a new combination proposed. Two locally distinguishable races can be identified with a gradual interflow into the typical *W. meriana* form. Variation is discussed and a distribution map and description are given.

Uittreksel

STUDIES IN DIE GENUS *WATSONIA* MILLER

Die *Watsonia meriana* (L.) Miller kompleks word beskryf en 'n nuwe kombinasie word gemaak. Twee plaaslike rasse kan geïdentifiseer word. 'n Inmekaar vloei van die rasse in die tipiese *W. meriana* vind egter plaas. Variasie in die kompleks word bespreek en 'n verspreidingskaart en beskrywing word gegee.

Introduction

The main object of this paper is to clarify the long existing controversy on the identity of *Watsonia meriana* (L.) Miller, *W. humilis* Miller and *W. coccinea* Herb. ex Klatt.

The identity of each of these species is very vague and this is emphasised when examining determined material in herbaria. In the past species were kept up by a description or a plate. Today extensive fieldwork is done and it is only now that it is realised that variation in plants plays an important role.

During the study of this species complex it was realised that variants of *W. meriana* formed the two last-named species dealt with in this paper.

Extensive variation is experienced throughout the distribution. *W. humilis* Miller and *W. coccinea* Herb. ex Klatt occur as two distinct ecological races throughout the main distribution range where these species occur, and in which the variation is fairly stable. Extensive variation is however experienced within these forms when found not within the range of these ecotypes.

A new combination is thus proposed where *W. humilis* Miller and *W. coccinea* Herb. ex Klatt are now cited as synonyms of *W. meriana* (L.) Miller.

A brief historical background of the three species involved is given to provide a better understanding of the proposed combination.

The possibility of hybridisation is considered in a brief discussion.

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HISTORY

Together with a plate by Ehret, Trew described and published *Watsonia meriana* in his *Plantae Selectae* in 1750. He published it under the name *Meriana florae rubello*.

Miller in the 6th edition of his *Gardeners Dictionary* (1752), published a description of a plant raised by him from seed, as *Watsonia meriana floribus infundibuliformibus subaequalibus*. In the 7th edition of his *Gardeners Dictionary* (1758) Miller published another phrase name for this plant, namely *Watsonia foliis ensiformibus, floribus alternis*. The same year (1758) Miller's *Figures of plants described in the Gardeners Dictionary* was published. Figure 276 of the 2nd volume is this plant. Then in 1768, in the 8th edition of his *Gardeners Dictionary,* he incorporated for the first time the Linnaean binomials naming his plant *Watsonia meriana*. He also published *W. humilis* as a new species with a figure (t.297 f.2).

However, in the 10th edition of the *Systema Naturae* (1759), Linnaeus published the former species *(W. meriana)* with the name *Antholyza meriana* with a reference to Trew's plate (t.40).

In 1762 Linnaeus's *Species Plantarum* ed. 2 was published and again included *Antholyza meriana* mentioning Trew's plate but not Miller's for Linnaeus would not recognise it as *Watsonia* but only as a part of *Antholyza*.

The 12th edition of the *Systema Naturae* was published in 1767 and Linnaeus cited Miller's *W. humilis* as a synonym for his *Antholyza meriana* var. *β minor*. Linnaeus believed that *W. humilis* Miller was a smaller form of his *A. meriana*.

Burman f. in the *Prodromus* to his *Flora Indica* based his *Antholyza meriana* on the same type as Linnaeus's *A. meriana* (Trew, t.40).

Linnaeus published his second *Mantissa* in 1771 and included Miller's *W. humilis* under *Antholyza meriana*, as he had decided it had no taxonomic rank at all.

However, in the 13th edition of Linnaeus's *Systema Vegetabilium* (1774) he mentioned Miller's *Watsonia meriana* as a synonym of his *Antholyza meriana* and with a detailed description published *Antholyza merianella*, citing Miller's *W. humilis* (t.297 f.2). He thus continued his refusal to recognise the genus *Watsonia*, but he did now recognise Miller's two species. The plant which he used for his description was what he believed to have been the same as Miller's *Watsonia humilis* but it was in fact a specimen of *Homoglossum merianella* (Milne-Redhead, 1938), a plant which is kept in the LINN-herbarium as No. 60.7 (De Vos, 1976).

Houttuyn published his *Natuurlijke Historie* in 1780 and cited Miller's plates for *Antholyza meriana* and for *Antholyza merianella*.

Murray published the 14th edition of the *Systema Vegetabilium* in 1784, incorporating all the new species from the *Supplementum* and in this edition

Miller's *W. meriana* and *W. humilis* were cited for his *Antholyza meriana* and *Antholyza merianella* respectively.

Thunberg's *Dissertatio de Gladiolo* was published the same year; he did not recognise Miller's genus *Watsonia*, nor did he recognise *W. meriana* and *W. humilis* as members of the genus *Antholyza* as Linnaeus had, but placed *Watsonia* species described to date in the genus *Gladiolus. Watsonia meriana* thus became *Gladiolus merianus* and *Watsonia humilis* became *Gladiolus marginatus* var. *sanquineus*.

Aiton in the first edition of the *Hortus Kewensis* accepted Linnaeus's *Antholyza meriana* and *Antholyza merianella*.

Jacquin's *Icones Plantae Rariores* was published between 1789 and 1797 and he too suppressed the genera *Antholyza* and *Watsonia*. Plate 229 is that of *Watsonia meriana* and plate 231 *Watsonia humilis*, but the latter was named *Gladiolus laccatus*.

In 1794 Thunberg's *Prodromus Plantae Capensis* appeared and in this he now only mentioned *Gladiolus merianus* and not *Gladiolus marginatus* var. *sanquineus* which was mentioned before by him in his *Dissertatio de Gladiolo.*

Willdenow in the *Species Plantarum* ed. 4 (1797) mentioned *Gladiolus merianellus, Gladiolus merianus* and *Gladiolus laccatus.* Only *G. merianellus,* a synonym for *W. humilis,* is related to this paper, as with *G. merianus* he cited several non-relevant species and his *G. laccatus* is a *Homoglossum*.

Curtis had by now started publishing his *Botanical Magazine* but it was only in 1798 that he described and figured the first *Watsonia* under the name *Antholyza meriana*. Ker however, in 1803, accepted the genus *Watsonia* and described *W. humilis.*

Ker in the 1st volume of *König & Sims Annals of Botany* (1805) revised the now accepted genus *Watsonia* naming *W. meriana* and *W. humilis*. In *Curtis's Botanical Magazine* of 1809 he published as t.1195 what he (Ker) believed to be a variety (β) of of *Watsonia humilis* and as t.1194 a small form of *Watsonia meriana.*

In 1809 Willdenow in his *Enumeratio plantarum horti Berolensis* still referred *W. meriana* to the genus *Gladiolus*; Aiton however in the 2nd edition of *Hortus Kewensis* accepted the genus *Watsonia*.

The 6th volume of Redouté's *Les Liliacées* was published in 1812. His *Gladiolus laccatus* is a synonym for *W. humilis*.

Sweet (1818) accepted both the genus *Watsonia* and the two species in his *Hortus suburbanus Londinensis* but Link referred these plants to the genus *Ixia* in his *Enumeratio Hortus Berolinsis* (Lewis, 1962).

Sweet in 1827 published his revision of the genus *Watsonia* in the *Hortus Britannicus* and cited Ker's *W. humilis* var. β as a form of *W. humilis* with no rank.

Klatt in *Linnaea* **32** agreed with this but later changed his mind, for in 1882

when he published his *Ergänzungen*, he used *W. humilis* var. β (t.1195, of the *Botanical Magazine*) as a reference to his *W. maculata* and validated the name *W. coccinea*, with t. 1194 as type, as proposed by Herbert in his MS.

Baker published his much needed revision of the long neglected *Iridaceae* in the 16th volume of the *Journal of the Linnaean Society* in 1877. Here he treated *W. meriana* and *W. humilis* as distinct species, with *W. coccinea* as a variety of *W. meriana*.

In the *Handbook of Irideae* he raised *W. coccinea* to specific level and did so again in 1896 in Thyselton-Dyer's *Flora Capensis*.

It is thus clear that a great deal of confusion existed amongst botanists. Plants already described and variants of these were in many cases given new names.

The last work, Baker's revision in 1896, gave each of these three species specific rank but today more is known about the distribution, ecology and variation of these plants.

During the study of the three species involved an attempt was made to keep them on either specific or varietal level, but no character/s occur in this complex to separate them from one another. Baker's concept of species involved could therefore not be upheld.

Distribution

The northernmost distribution of *W. meriana* is on the higher parts of the Kamiesberg and it then streches further south along the coastal belt and interior west of the Bokkeveld and Sederberg down into the South-Western Cape and as far east as Bredasdorp. (Fig. 1).

The species is found through a range of vegetation and soil types and this together with climatological conditions has resulted in two almost distinct races.

The Typical *Watsonia meriana* (L.) Miller Form

This more common large form of *W. meriana* is regarded as the typical form as it corresponds best to Trew's plate (t.40) and that of Miller (t.276). Linnaeus cited t.40 for his *Antholyza meriana* and it is in fact the lectotype of *W. meriana*.

This form inhabits the dry karroid conditions in the most northern limits (3018—Kamiesberg) of its distribution as well as in the south-eastern (3119—Calvinia and 3319—Worcester) limits of its distribution. It also ranges through renosterbos and sandveld on the coastal belt (3218—Clanwilliam) and parts of the interior (3318—Cape Town) of the south-western Cape.

The plants grow in a variety of soil types. Old granite is represented in the Kamieskroon district, with the Dwyka Series of the Karroo System on the escarpment between Nieuwoudtville and Vanrhynsdorp. Coastal sands on the westcoast and sand derived from the Table Mountain Series are found in the interior south of Klawer and are mainly confined to the mountain ranges that

FIG. 1.
Distribution of *Watsonia meriana* (L.) Miller.

● – The typical *Watsonia meriana* (L.) Miller.
■ – The *"Watsonia humilis"* race.
▲ – The *"Watsonia coccinea"* race.

stretch down to the coast at Hermanus in the south. Malmesbury Shale is found from Piquetberg to south of Malmesbury, as well as the flats and lower foothills between Worcester and Robertson.

Although classified as a winter rainfall region, rain is frequent throughout the year with the main precipitation occurring between June and August. An average rainfall of between 200 and 250 mm p.a. is recorded in the northern regions with the exception of over 300 mm on the Nieuwoudtville escarpment. From Malmesbury south to the Cape Flats (3318—Cape Town) 450–550 mm p.a. is recorded.

The plants which grow in areas where water may collect in shallow pans during the rainy season are taller than those from drier areas; a fair amount of variation is found throughout the distribution.

This deciduous species grows mainly in small clusters, rarely as individuals, and large masses are found in seasonally moist, almost vlei conditions in the Darling area. In these colonies the plants usually have narrow erect leaves, whereas plants from the drier parts and sandveld usually have broad ensiform leaves spreading in a fan shape. Leaves in the karroid areas usually have much thickened prominent margins.

Corms are usually large and tunicated with a hard coarse fibre which forms several layers.

A colony of the dwarf form of the typical *W. meriana* is found in the sandveld on the farm "Kleindiamant" south of Malmesbury and here the plants tend to grow more as separate individuals.

This form flowers from September to October.

A diploid chromosome number of 18 (Goldblatt, 1971) is present in this typical form.

Distinguishable Races

Watsonia humilis Miller and *Watsonia coccinea* Herb. ex Klatt are regarded as separate races. The reason for this is that these formerly two separate species are only distinguishable by their distribution and flower colour.

The "*W. humilis*" race is found on the Cape Peninsula with only one known colony in the sandveld between Cape Town and Malmesbury where it grows in temporary wet conditions which are only slightly saline. In this colony the plants are taller and flower earlier than those on the higher altitudes, and flowers are pale translucent pink.

This form grows in conditions which are wet for almost the entire year. At Cape Point, at an altitude of 150 m, it is fairly common. It is also common at Woodhead on Table Mountain at an altitude of 747 m. The rainfall increases from 333 m at Cape Point to 1 620 mm p.a. at Woodhead.

Plants of this race usually grow as separate individuals scattered over large areas. The leaves in most cases are short, linear, erect or spreading. The spike can be simple or branched. A simple spike can consist of as few as 2 flowers and a

branched spike with as many as 10 flowers. The corm is small and tunicated with fine fibre which forms several layers.

Collections made at Bergvliet and Kenilworth are much taller with long erect linear leaves and compare well with the colony in the sandveld north of Cape Town.

Flowering occurs from October to November at the higher altitudes. The flowers are pink (Royal Hort. Soc. colour chart No. 55b) throughout the race. Capsules are broad ellipsoid in cases where plants are found in the wetter areas but become longer and narrower in drier conditions. Seed is shed in March and April.

Goldblatt (1971) reported a diploid chromosome number of 18 in this race.

The *"Watsonia coccinea"* race occurs in the southern distribution range of this species complex and is distinct from the typical *W. meriana* as it always grows individually and never forms clusters. The soils derive mainly from Table Mountain and Bokkeveld Series with limestone south-east of Bredasdorp.

Rainfall measures from 470 mm at Bredasdorp at an altitude of 67 m, to 920 mm at Highlands at an altitude of 366 m.

The conditions in which the race is found, are very marshy for most of the year but tend to dry out completely to the south. The plants are relatively stable under these conditions, but are more slender with longer and narrower leaves at higher altitudes when growing in drier conditions. Plants are scattered as individuals over vast areas.

The small corm is tunicated with fine fibre. Plants growing in drier conditions tend to have bigger corms.

The flowering period is from September to October and the colour is always orange (Royal Hort. Soc. colour chart No. 33a). Frequent burning improves flowering. Seed capsules are broad ellipsoid.

Hybridisation

Continual variation might lead to the idea that hybridisation may occur. But, in the many collections made and in the colonies studied in areas where the *W. humilis* and *W. coccinea* races occur, the author has observed no significant variation in single colonies to suggest that more than one parent could be involved.

Seedset is good in all populations investigated.

Plants of the typical *W. meriana* collected in the veld in most cases show little variation or change when brought into cultivation. Exceptions, as in the case of *W. meriana* (dwarf form) which when cultivated increased considerably in size, do occur. This is also the case with *"W. coccinea"* race when corms were brought into cultivation or when raised from seed.

Plants raised from seed showed no extensive degree of variation. In the case of an F2 hybrid population a maximum of ± 12% of the plants should show some form of original parentage which in this case did not occur.

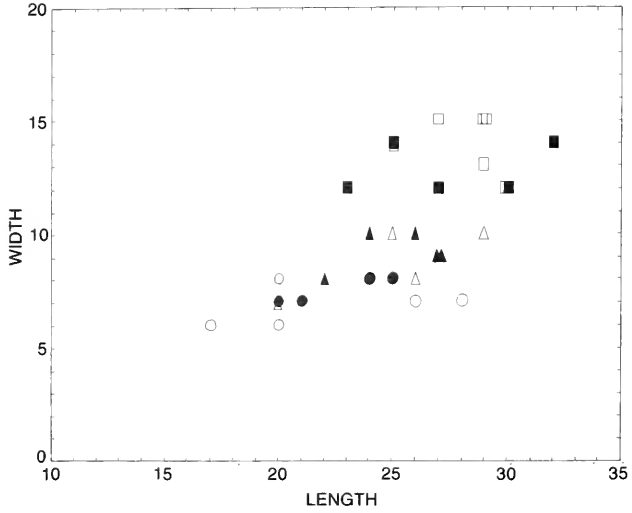

FIG. 2.
Variation of bracts and bracteoles in the three *Watsonia meriana* races.

Typical *W. meriana*.
○ – Bracts
● – Bracteoles

"W. humilis" race.
□ – Bracts
■ – Bracteoles

"W. coccinea" race.
△ – Bracts
▲ – Bracteoles

The possibility that F1 hybrid populations do occur is remote. The author believes it is not possible for a hybrid population, for instance in the case of *"W. coccinea"*, to stretch over a distance of ± 120 km.

Also the absence of possible parent plants throughout the distribution area leads one to believe that these Watsonias are ecological forms.

VARIATION

Due to the large amount of variation in the vegetative parts of this complex it was impossible to work on any vegetative characters. The floristic parts, e.g. bracts, bracteoles and the outer and inner perianth segments were used to plot the variation as these proved to vary only slightly.

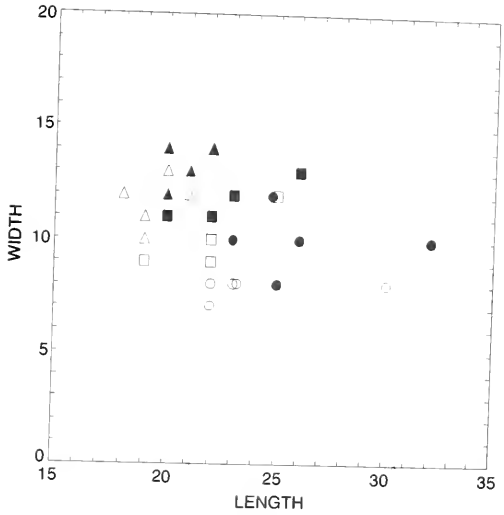

FIG. 3.
Variation of the outer and inner perianth segments in the three *Watsonia meriana* races.

Typical *W. meriana.*
○ – Outer segments
● – Inner segments

"W. humilis" race
□ – Outer segments
■ – Inner segments

"W. coccinea" race
△ – Outer segments
▲ – Inner segments

Figure 2 shows the variation of the bracts and bracteoles of five specimens of each of the three forms. The typical form of *W. meriana* from Darling, the *"W. humilis"* race from Steenberg plateau and the *"W. coccinea"* race from Betty's Bay were used.

Figure 3 shows the variation of the outer and inner perianth segments of the same forms from the same localities used in Figure 2.

The interflow of characters in the three forms is clearly visible which makes it thus impossible to separate them on specific or varietal level. They can be regarded as locally distinguishable races only.

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Antholyza merianella Houtt. in Nat. Hist. **2**(12): 61 (1780) non L.; Murray in L. Syst. Veg. ed. 14: 87 (1784) non L.; Ait. in Hort. Kew. ed. 1: 67 (1789) non Murray.

Gladiolus marginatus var. *τ sanquineus* Thunb., Diss. Glad.: 18 (1784) non L.f.

Gladiolus merianus Jacq., Ic. Plant. Rar. 2, t.229 (1789): Red., Lil. **1**: 11, t.11 (1802); Willd., Enum. plant. Berol.: 60 (1809); Thunb., Fl. Cap. ed. Schultes: 40 (1823) excl. syn. Jacq.

Gladiolus laccatus Jacq., Ic. Plant. Rar. 2, t.231 (1789); Red., Lil. **6**: 343, t.343 (1812).

Gladiolus merianellus Willd. Sp. Plant. **1**: 214 (1797) excl. syn. L.

Watsoina meriana var. *τ* Ker in Bot. Mag. t.1194 (1809).

Watsonia humilis var. *β* Ker in Bot. Mag. t.1195 (1809).

Ixia meriana Link, Enum. hort. Berol. **1**: 52 (1821) f. Lewis.

Watsonia maculata Klatt, Ergänz.: 17 (1882).

Watsonia meriana (L.) Miller var. *coccinea* Herb. ex Bak. in J. Linn. Soc. Bot. **16**: 158 (1877).

Watsonia coccinea Herb. ex Klatt, Ergänz.: 18 (1882); Bak. in Handb. Irid.: 175 (1892) & in Dyer's Fl. Cap. **6**: 101 (1896).

Pre Linnaean:

Meriana florae rubello Trew, Plant. Selec.: 11, t.40 (1750).

Watsonia meriana floribus infundibuliformibus subaequalibus Miller, Gard. Dict. ed. 6, Ic.4 (1752).

Watsonia foliis ensiformibus, floribus alternis Miller, Gard. Dict. ed. 7, 1c.2, t.276 (1759).

Plants very variable in size. *Corm* 40–70 mm diam., with neck to 60 mm long; densely tunicated with hard, coarse, pale to dark brown fibre which forms 3–5, often more layers. *Stem* erect, firm and usually not flexuose, often simple in dwarf forms but usually with 1–7 erect, often flexuose branches, stem 220–1 380 mm tall. *Leaves* herbaceous and distichous and spread fan-shaped to erect, firm, 2–7 but usually 4, ensiform to linear, leaves with thickened midrib which is generally not very prominent, venation distinct, margins slightly, often much thickened, 110–730 mm long × 4–44 mm wide. *Cauline leaves* 2–4, ensiform to linear, sheathing stem for most of its length, lower cauline leaves inflated, upper sheathing, often overlapping. *Spike* to 440 mm long, simple or branched, often flexuose, 1–7 branches, erect, distichous; main spike dense to lax, to 440 mm long, 1–17 flowered. *Bract* 17–38 mm long × 5–13 mm wide, herbaceous with apex usually dried out, bracts not overlapping, clasping stem at base only, usually shorter than bracteoles but often as long, lanceolate, acute to obtuse often emarginate. *Bracteole* 12–39 mm long × 6–11 mm wide, usually longer than bracts, herbaceous to membranous with apex usually dried out, lanceolate, acute to obtuse, often bidentate. *Perianth tube*: basal part filiform, straight or slightly curved, widening only slightly, 13–34 mm long, upper part cylindrical, curved and slightly widening, 20–35 mm long. *Segments*: outer, obovate to elliptic, 19–30 mm long, 6–17 mm wide; inner, obovate, 19–32 mm long × 7–15 mm wide. *Stamens* 33–70 mm long, arcuate. *Staminodes*: absent in this species of *Watsonia*. *Anthers* 6–12 mm long, linear saggitate, all facing lower perianth segment. *Ovary* obovate, 3–6 mm long, 2–3 mm diam. *Style* filiform, 62–88 mm long, pale. *Stigmatic branches* filiform, 4–7 mm long, linear, obtuse, often overtopping anthers. *Capsule* 36–55 mm long × 9–11 mm diam., narrow to broad ellipsoid.

Flowers from September to November. Colour range recorded, Royal Hort. Soc. colour chart no. 19d, 26a, 28a, 29a, 29c, 30c, 31a, 36a, 37a, 38c, 41d, 45a, 45b, 48a, 49a, 55a, 56a, 56c.

Specimens Examined

CAPE—3018 (Kamiesberg): Kamiesberg, Little Namaqualand (-AC), *s.n.* NBG *1813/32* (BOL); Kamiesberg between Garies and Leliefontein, *Esterhuysen 1394* (BOL); Welkom, Kamiesberg near Garies, *Esterhuysen 23719* (BOL); Garies (-CA), *Horn s.n.* (NBG *61837*).

——3118 (Vanrhynsdorp): Between Vanrhynsdorp and coast (-DA), *Pillans s.n.* (BOL); Gifberg, Vanrhynsdorp (-DC), *Phillips 7517* (SAM); Gifberg, Vanrhynsdorp, *Phillips 7627* (NBG).

——3119 (Calvinia): Nieuwoudtville, Calvinia (-AC), *Compton s.n.* NBG *61833* (NBG).

——3218 (Clanwilliam): Graafwater, Clanwilliam Div. (-BA), *Zinn s.n.* SAM *59721* (SAM); Sandveld between Grey's Pass and Graafwater, *Leipoldt 3574*

(BOL); Olifants River Valley, 5 miles N. of Citrusdal (-BB), *Lewis 1368* (SAM); Brandberg, between Sandberg and Graafwater (-BC), *Rourke 1566* (NBG); Marsh on N.E. margin of Verloren Vlei (-DA), *Pillans 7799* (BOL); Scherpeheuvelsberg near Grey's Pass, *Leipoldt* (SAM); Near Sauer, Piquetberg (-DC), *Barker 8089* (NBG); South of Sauer in dry sandy soil (-DD), *Lewis 3559* (SAM).

——3219 (Wuppertal): Brakfontein, between Citrusdal and Hex River (-CA), *Bolus* (BOL).

——3318 (Cape Town): Rocky hill S. of Langebaan (-AA), *Pillans 6700* (BOL); 2 miles from Ysterfontein, *Hall 162* (NBG); Hopefield (-AB), *Middlemost s.n.* NGB *61842* (NBG); Farm ''Oubos'' near Darling (-AD), *Roux 201* (NBG); At turnoff to Darling from Cape Town. Malmesbury road (-BC), *Roux 199* (NBG); Junction to Malmesbury, Darling-Mamre road, *Roux 202* (NBG); 15 km. E. of Mamre Rd. station, along road (-CB), *Roux 200* (NBG); Sandy flats between Malmesbury and Darling, *Pillans 6709* (BOL); Klaver Vlei, Darling, *s.n.* BOL *19150* (BOL); Darling, *s.n. 430/14* NBG (BOL); Mamre, *Bolus* (BOL); Camps Bay, Cape Town (-CD), *Zeyher s.n.* SAM *48529* (SAM); 18 miles from Cape Town along Melkbosch road (-CD), *Lewis* (SAM); Kenilworth race course, *Lewis 478* (SAM); Melkbosch road, *Olivier s.n.* NBG *61835* (NBG); Kenilworth race course, *Lewis 56* (SAM); Table Mountain, W. side of upper plateau, *Stokoe* (SAM); Kenilworth race course, *Cross 75* (SAM); Table Mountain, between Kasteels Poort and Woodhead, *Roux 250* (NBG); Flats near College Range, *Wolley Dod 642* (BOL); Rosebank, *s.n.* BOL *3800* (BOL); Table Mountain, *s.n. 1790/25* NBG (BOL); Hely Hutchinson Reservoir (-CD), *s.n. 1789/25* NBG (BOL); Table Mountain, *Taylor 1303* (BOL); Table Mountain, near Woodhead, *Goldblatt 405* (BOL); Claremont Flats, *Mathews* (BOL); Kenilworth race course, *Esterhuysen 32054* (BOL); Rapenburg, Mowbray, *Guthrie 132* (BOL); Killarney Flats, *Lewis 5553* (NBG); Camp Hill Village turnoff, 20 km. S. of Malmesbury, *Goldblatt 2320* (NBG); Table Mountain, *Pillans 1253* (BOL); Kuils River (-DC), *s.n. 2141/27* NBG (BOL); Between Stellenbosch and Paarl, *Ryder* (BOL); Kraaifontein, *Robinson s.n.* SAM *61845* (SAM); Joostefontein Paarl Div. (-DD), *s.n. 1569/25* NBG (BOL); Stellenbosch Div. *s.n.* BOL *17868* (BOL).

——3319 (Worcester): French Hoek (-CC), *s.n. 1202* Univ. Gardens Stellenbosch (BOL); Stettynskloof, Worcester (-CD), *Barker 9453* (NBG); Scherpenheuvel Vlei, (-DA), *Barker 7516* (NBG); Boesmans Kloof Pass at McGregor (-DD), *Leipoldt 3573* (BOL); McGregor, *Barker 1983* (NBG).

——3418 (Simonstown): Steenberg Plateau (-AB), *Lewis 798* (SAM); Bergvliet farm, Camp near Albertyns, *s.n.* SAM *90129* (SAM); Bergvliet farm (a) 3 beacons, (b) near pump, *Purcell 151* (SAM); Bergvliet farm (a) three beacons (b) camp near Albertyns, *Purcell s.n.* SAM *90131* (SAM); Bergvliet farm, near sandpit, *Purcell s.n.* SAM *90132* (SAM); Silvermine Plateau, *Walters 218* (NBG); Steenberg, *Barker 3305* (NBG); Muizenberg Mt., *Barker 4209* (NBG); Noordhoek Mt., *Compton 14031* (NBG, BOL); Smitswinkel Flats (-AD), *Comp-*

ton 14008 (NBG); Cape Point, *Compton 12320* (NBG); Near Klaasjagers, *Steyn 658* (NBG, BOL); Smitswinkel Bay, *Salter* (BOL); Cape Flats (-BA), *Scott Elliot 1189* (NBG); Cape Flats (-BA), *s.n. 2569/34* NBG (BOL); Hottentots Holland Mts. (-BB), *Pappe s.n.* SAM *48593* (SAM); Hottentots Holland, *Pappe s.n.* SAM *48590* (SAM); Highlands, *Compton 13489* (NBG); Highlands Est. *Lewis 2006* (SAM); Highlands near Elgin, *Linley* (SAM); Highlands, *Leighton 285* (BOL); Sir Lowry's Pass, *s.n.* BOL *5559* (BOL); Firgrove Flats, *Martley* (BOL); Above Kogelbay (-BD), *Barker 3244* (NBG); Sandy flats near Pringle Bay, *Lewis 1602* (SAM); Hangklip Convict Station, Caledon, *Barker 3923* (NBG); Between Hangklip and Betty's Bay, *Hiemstra 685* (NBG); Hangklip, *Loubser 498* (NBG); Harold Porter Botanic Garden, Betty's Bay, *Ebersohn* (NBG); Road to Ou Bos, Hangklip Estate, *Leighton 286* (BOL).

——3419 (Caledon): Houwhoek (-AA), *Zeyher s.n.* SAM *48592* (SAM); Elgin, *Compton s.n.* NBG *61846* (NBG); Zwartberg, Caledon (-AB), *Templeman s.n.* SAM *211057* (SAM); Caledon, *Loubser 388* (BOL); Dieprivier Caledon, *Martley* (BOL); Fransche Kraal swamp (-CB), *Barker 8501* (NBG); Between Gansbaai and Danger Point, *Stokoe* SAM *55631* (SAM); Hermanus (-AC), *Loubser 892* (NBG); Near Elim (-DA), *Martin 602* (NBG); Near Elim, *Barker 5578* (NBG); Hills near Elim, *Guthrie 3525* (BOL); Elim, *s.n.* BOL *6839* (BOL).

——3420 (Bredasdorp): The Poort, Bredasdorp (-CA), *Compton 9030* (NBG); The Poort, Bredadsdorp, *Wasserfall 396* (NBG, BOL).

Without precise locality:

Flower show, Hermanus, *Rev. F. A. Rogers s.n.* SAM *29061* (SAM); Wild flower show, Cape Town, *s.n.* SAM *28439* (SAM); Ex Hort. Kirstenbosch *s.n.* NBG *61839* (NBG); *Zeyher s.n.* SAM *48536* (SAM); *s.n.* SAM *48538* (SAM); *s.n.* SAM *48533* (SAM); *s.n.* BOL *18469* (BOL); Cape wild flower show *s.n.* BOL *13765* (BOL); Ex Hort. Kirstenbosch *s.n. 637/13* NBG (BOL); Ex Hort. Kirstenbosch *s.n.* BOL *17868* (BOL).

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AN ANNOTATED REVISION OF THE GENUS *SCHIZOCHILUS* SOND. (ORCHIDACEAE)

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Abstract

The genus *Schizochilus* (Orchidaceae) is revised. Ten species and three subspecies are recognised. Two new species are described: *S. lilacinus* and *S. crenulatus*. The history, morphology and systematic position of the genus are briefly reviewed, and the available information on the habitats of each species is compiled. Two species are illustrated.

'N GEANNOTEERDE HERSIENING VAN DIE GENUS *SCHIZOCHILUS* SOND. (ORCHIDACEAE)

Uittreksel

Die genus *Schizochilus* (Orchidaceae) word hersien. Tien spesies en drie subspesies word erken. Twee nuwe spesies word beskryf: *S. lilacinus* en *S. crenulatus*. Kort aantekeninge oor die geskiedenis, morfologie en die sistematiese posisie van die genus word gegee, en die beskikbare informasie oor die habitat van elke spesies word gegee. Twee spesies word geïllustreer.

Introduction

Schizochilus Sond. is a genus of 10 species. Despite the small size of the plants (rarely larger than 300 mm), the bright white and yellow flowers and the elegantly slender plants with nodding flower-heads make it one of the most beautiful groups of southern African terrestrial orchids.

The taxonomy of this genus has been in a state of confusion since the treatments by Rolfe (1912) and Schlechter (1921). However, these taxonomists ought not to be judged too harshly: *Schizochilus* shows extensive convergent evolution. The most common species *(S. zeyheri)* has a wide range of variation that segregates partially into geographic forms; and the flower morphology is remarkably uniform throughout the genus. From the limited herbarium material available at that time and, in Rolfe's case, the absence of field experience, no satisfactory treatment was possible. Unfortunately, Schlechter also created some nomenclatural confusion by describing numerous species and by misinterpreting some of Rolfe's concepts.

This study is an attempt at a biologically satisfactory classification, in which species are regarded as evolving biological entities, the products of still active processes. These processes concern adaptations to habitat and to pollinators. So, although my species conform to the traditional norms as set out in Davis and Heywood (1963), habitat, flower colour and phytogeography were extensively

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taken into account. To extend the data base of these non-traditional characters, extensive field work was done in the summers of 1976–77 and 1978–79. Populations of all species except *S. lepidus* Summerh. and *S. cecilii* Rolfe ssp. *cecilii* were investigated.

It is unfortunate that the cultivation of the orchids still presents so many problems, as biosystematic studies—especially with regard to the fertilisation systems—could reveal valuable and interesting information on the adaptive strategies and survival capacities of these taxa.

Historical Review

The genus *Schizochilus* Sond. was described in 1847, with *S. zeyheri* as the only species. During the next 60 years, only two more species were added: *S. bulbinella* (Reichb.f.) H.Bol. and *S. gerrardii* (Reichb.f.) H.Bol. But during this period the status and affinities of the genus were under constant review. Most taxonomists did not accept it as an independent genus. Reichenbach (1867) included it in *Brachycorythis* Lindl., Schlechter (1895) in *Platanthera* Rich. and Kraenzlin (1898) in *Gymnadenia* L.C.Rich. Initially the genus had been allied to the *Disa-Satyrium* group, but Schlechter linked it to the *Gymnadenia* group, an opinion that is still widely followed. After Rolfe's revision (1912), *Schizochilus* has generally been accepted as an independent genus.

From 1905 to 1925 the number of described species in the genus increased from three to 26. Both Rolfe and Schlechter described every variant and local facies as a new species, of which most are based on single collections. Of the 13 new species, which Schlechter published in 1921, only one is upheld in the present revision, and that with subspecific status.

Although Schlechter's (1921) revision has been generally followed in herbaria, the need for a critical revision has long been realised (Dyer, 1944; Schelpe, 1966).

The Systematic Position of *Schizochilus*

Schizochilus belongs to the Orchideae (sensu Airy Shaw, 1973). Pfitzer (1889) placed the genus in the "Monandrae-Ophrydinae-Satyrieae" which included *Disa, Satyrium, Brachycorythis, Schizochilus* and *Platycoryne*. As sole differentiating character the angle between the anther and the ovary (acute in this group, obtuse in all other Ophrydinae) was mentioned.

Schlechter (1895) allied *Schizochilus* with the *Gymnadenia-Platanthera* group, on the basis of lip structure, general tepal orientation and rostellum structure. He diagnosed the group as: lip ligulate or trilobed, usually spurred; sepals and petals sub-equal, more or less ovate; anther relatively simple, erect; stigma flat or concave, usually vertical in the mouth of the spur; rostellum simple and small. This system was followed by Kraenzlin (1898), Rolfe (1912), Schlechter (1921, 1927) and Summerhayes (1968).

Senghas (1973) elaborated Schlechter's (1927) system, describing three tribes, of which the Orchideae are then subdivided into five subtribes. *Schizochilus* is included in the Platantherinae, together with *Brachycorythis, Platanthera, Gymnadenia* and *Holothrix*. The group is characterised by (a) a single concave stigma, and (b) by the glands being naked, not enclosed by bursiculae. The Platantherinae are further divisible into two subgroups, on the basis of rostellum structure. The *Gymnadenia* group is characterised by a rostellum with a central lobe that extends between the anther cells (*Schizochilus* belongs to this group). The *Platanthera* group does not have such a well-developed central rostellum lobe.

The differentiation of *Schizochilus* from its allied genera has consistently caused problems. Characters most frequently used are: (a) flower colour yellow or white (Kraenzlin, 1898), (b) flowers not resupinate (Kraenzlin, 1898), (c) presence of calli at the throat of the spur (Schlechter, 1921; Senghas, 1973), (d) inflorescences nodding (Schelpe, 1966), (e) tubers testicular (Senghas, 1973), (f) petals half as long as the sepals (Senghas, 1973; Rolfe, 1912) and rostellum trilobed (Schlechter, 1921). Flower colour and nodding inflorescences separate *Schizochilus* from the European *Nigritella* L.C.Rich., and non-resupinate flowers, testicular tubers and nodding inflorescences from *Gymnadenia*. Several species of *Schizochilus* have subobsolete or no calli, and the three-lobed rostellum is typical of the whole *Gymnadenia* group. *Schizochilus* is best differentiated by the following characters: tubers generally testicular, inflorescence usually nodding; petals ca. half as long as the sepals; lateral sepals suboblique; lip trilobed, the central lobe invariably longer than the lateral lobes; flowers white or yellow or pale mauve, not resupinate.

Phytogeography, Ecology and Systematics

By comparing the phytogeographical, ecological and morphological patterns shown by the taxa, an overall hypothesis on the evolutionary relationships within the genus *Schizochilus* can be constructed. This hypothesis is implied in the ranks and delimitation of taxa and in the sequence in which they are arranged.

Most of the genus occupies the Afro-montane Zone, as defined by White (1976, 1978a). Only *S. zeyheri* transgresses occasionally into Tongaland-Pondoland Region (White, 1976). Four centres can be recognised in the distribution of *Schizochilus*. These do not agree with the centres and intervals proposed by Weimarck (1941), who recognised a single Drakensberg centre and an interval between the Mlanje and Rungwe Subcentres. The major phytogeographical patterns are indicated in Figure 1.

In the Afro-montane Zone *Schizochilus* occurs in grasslands and rock flushes and on rock ledges. In the Guinea-Congolian Zone it occurs in edaphic grasslands. Within the Afro-montane Zone there is both an ecological as well as a geographical differentiation among species. The geographical differentiation can be between centres and in three cases, within centres. Ecological separation within a centre is

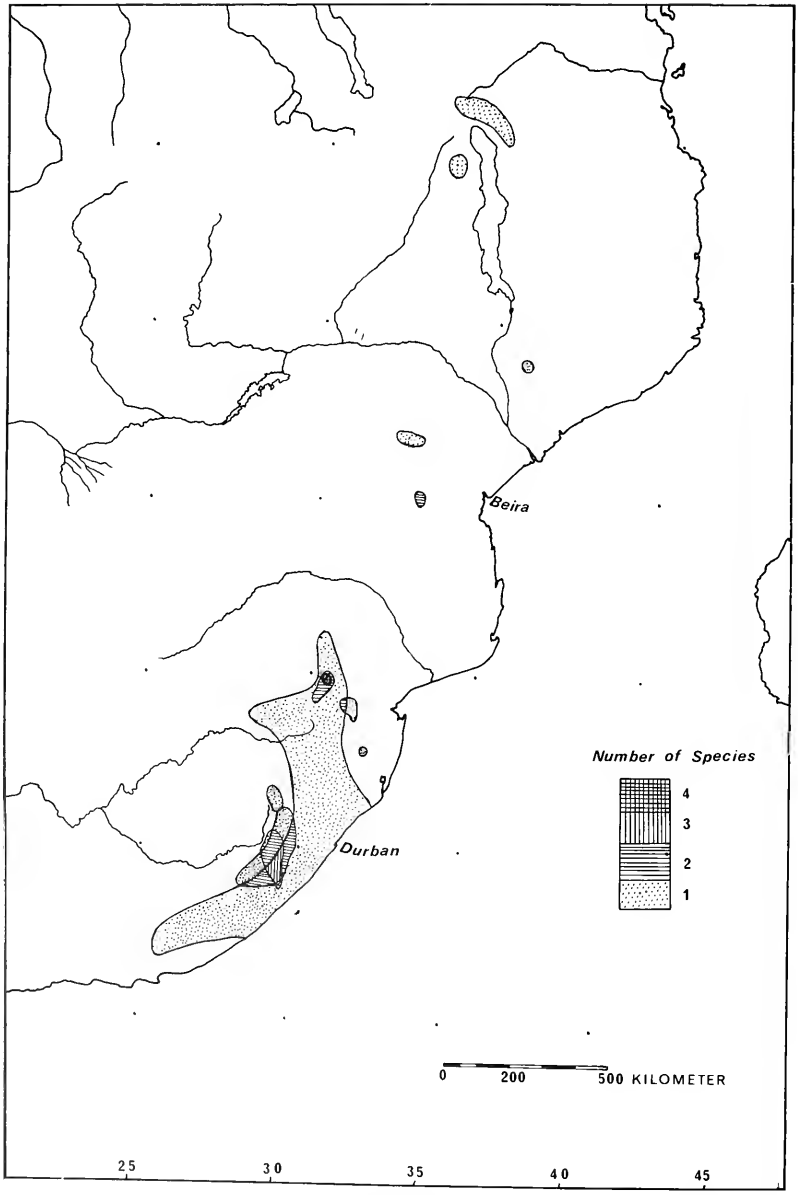

FIG. 1.
Distribution of the genus *Schizochilus* Sond., showing the concentration of species in the Drakensberg

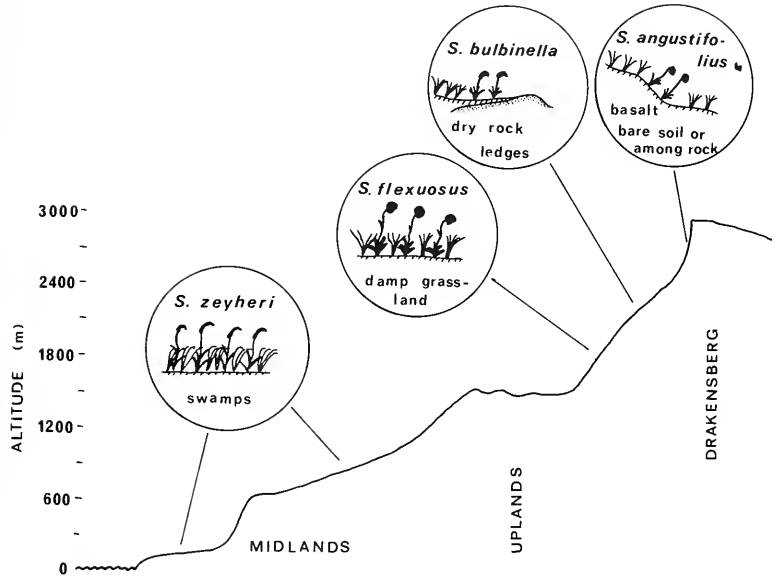

FIG. 2.
Ecological relationships among the species in the Natal Drakensberg and coastal areas

best indicated by a direct diagrammatic comparison of the habitats of each species. A comparison of habitats between centres is rather difficult, as no quantified habitat descriptions exist.

The habitats of the species of the Natal Drakensberg Centre are compared in Figure 2. Taxa separate altitudinally, but this altitudinal gradient probably reflects a complex of other environmental factors. Where altitudinal overlap of species occurs, (*S. bulbinella* and *S. flexuosus*, i.e. at Bushmansnek), the taxa inhabit different habitats. Note that the high-altitude taxa *(S. bulbinella* and *S. angustifolius)* are separated eco-geographically.

In the Transvaal Drakensberg specific habitats appear to separate more or less on a moisture gradient (Fig. 3). At Graskop *S. zeyheri, S. crenulatus* and *S. cecilii* ssp. *transvaalensis* were found in the same swamp, but each in its own habitat. Populations were not mixed. On Long Tom Pass *S. cecilii* ssp. *transvaalensis* and *S. lilacinus* were found in the same locality. *S. cecilii* ssp. *transvaalensis* and ssp. *culveri* appear to be geographic vicariants.

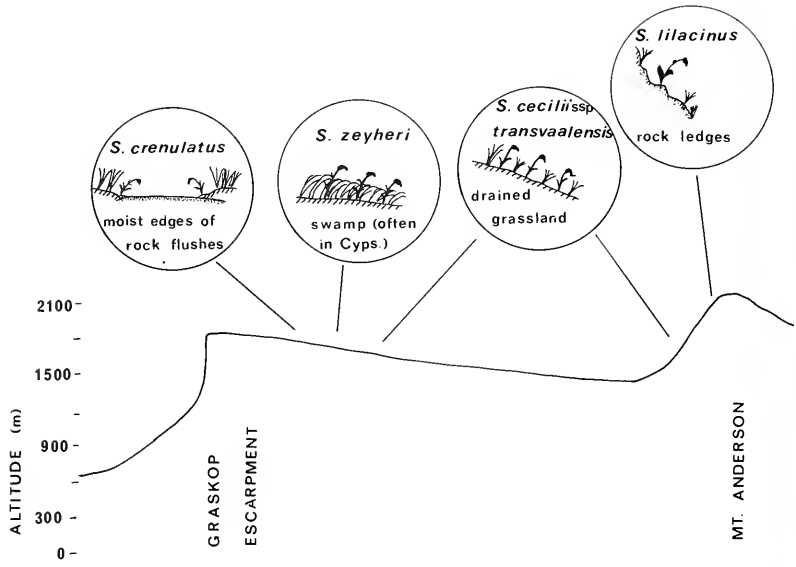

FIG. 3.
Ecological relationships among the species in the Eastern Transvaal escarpment mountains (Pilgrims Rest-Lydenburg area)

The Manica Centre is much poorer and there are not sufficient data to show ecological differentiation among the taxa. Two subcentres—the Inyanga subcentre and the Chimanimani subcentre—may be recognised, each with a single species.

The Southern Riftvalley mountains contain a single species—*S. sulphureus*.

The postulated evolutionary patterns based on morphological relationships are shown in Figure 4. According to this schema convergent evolution occurred in spur length, flower size and distribution of leaves on the scape. The variation in *S. zeyheri* is not indicated on the diagram. The data contained in this schema, combined with ecological and phytogeographical data, have been used to construct Figure 5. This is a hypothetical correlation of all these data to show the possible patterns in speciation in this genus.

DISCUSSION OF MORPHOLOGICAL CHARACTERS

Introduction

Almost all characters show both intra- and interspecific patterns of variation. Extensive variation in a character in one species does not reduce its value as a differential or essential character in another species. Correct species delimitations

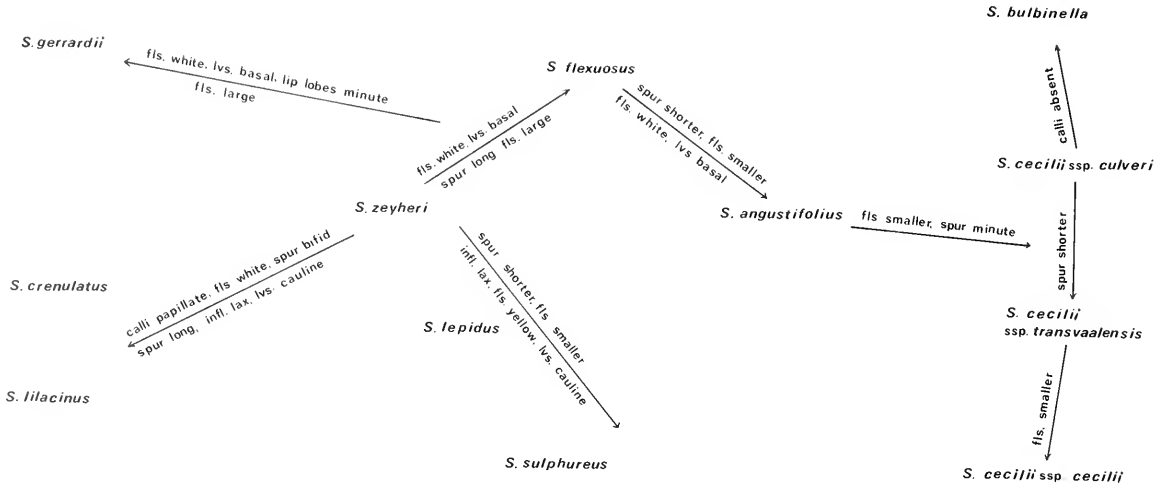

FIG. 4.
Postulated relationships among the taxa based on morphological evidence. The characters above the arrow apply to the species to which the arrow points, those below the arrow are common to the species both sides of the arrow.

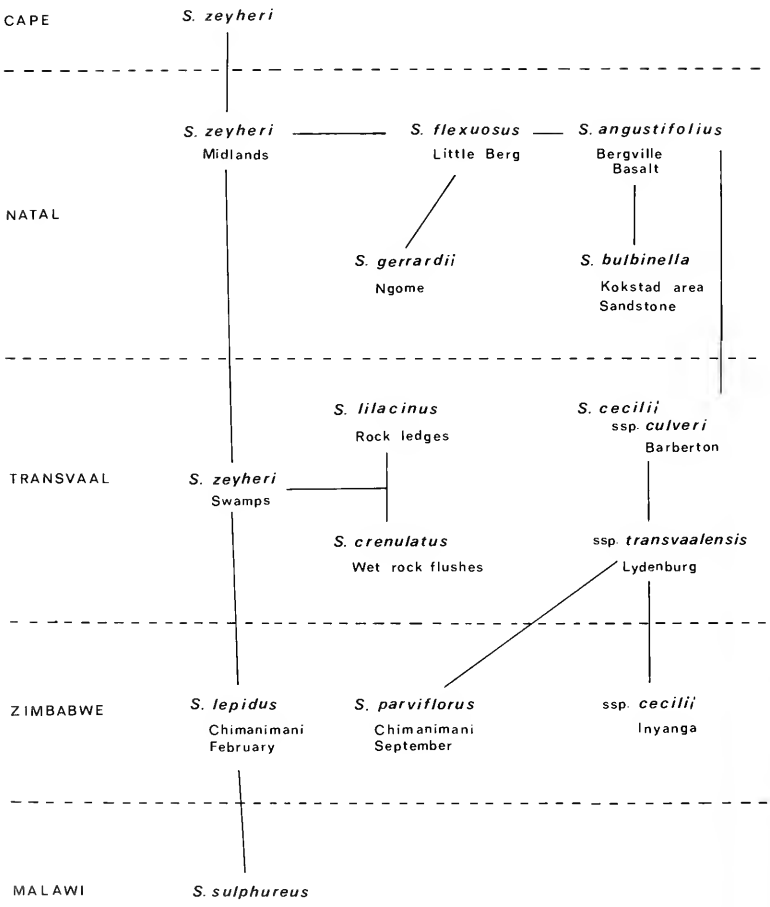

FIG. 5.
Postulated evolutionary relationships based on morphological, ecological and phytogeographical data. Eco-geographical characters separating closedly related species are given below the species name.

depend on the careful separation of intra- and interspecific variation. Supra-specific groupings, in turn, depend on an understanding of variation patterns within the genus. Failure to study the variation patterns critically led to the description of numerous species in the past.

Leaf Morphology

(a) *Leaf shape* ranges from linear to ovate. In taxa such as *S. cecilii* ssp.*transvaalensis, S. zeyheri* and *S. bulbinella* variation is immense, but for *S. lilacinus* and others it is excellent as a differential character. This character has been used uncritically in the past.

(b) *Distribution of leaves*. Although it has taxonomic importance, this character is difficult to quantify. The laminate leaves (as opposed to the sheathing leaves) can either occur in a basal cluster (i.e. *S. flexousus, S. gerrardii*), or be scattered on the lower half of the scape (i.e. *S. zeyheri, S. cecilii* ssp. *cecilii*). In depauperate or badly dried specimens, it is frequently difficult to assign a character-state. Although intermediate forms also occur, in the vast majority of the material leaf position is a good character.

Inflorescence Shape

Inflorescence shape is determined by the density and the length of the inflorescence. Density of the inflorescence forms a good character, provided the intermediate state of some taxa is recognised (i.e. *S. lilacinus*). In this work a dense inflorescence is understood as one in which the scape is entirely obscured by floral bracts and flowers. The opposite is a lax inflorescence. The length of the inflorescence determines whether the shape is capitate or oblong. Capitate inflorescences only occur in *S. angustifolius* and *S. flexuosus*, but intermediate states do occasionally occur.

Sepals and Petals

For a genus of 10 species, these floral characters show remarkably little variation. The more peculiar species in the genus do vary: *S. lilacinus* has very narrowly lanceolate sepals and small petals. In the larger-flowered specimens of *S. flexuosus* and *S. zeyheri*, the petal shape changes somewhat—but this appears to be due to the larger flowers. Schlechter (1921) used petal shape to some extent, but without a knowledge of the range of variation displayed by this character.

Spur and Lip

This structure provides a wealth of data that was used extensively in previous attempts at classifying the genus. The lip is a complex structure, for which no satisfactory nomenclature is available. The nomenclature followed in this work is elucidated in Figure 6. In this I am following Summerhayes (1968), but the

terms used do not imply homology to other genera with similarly named structures. Variation occurs in the following structures:

(a) *Callus*. The presence or absence of a callus and usually the shape of the callus, is consistent within a species. It is a minute structure and difficult to interpret in dried material.

(b) *Lateral lip lobes*. These can vary from being half the size of the central lip lobe, to being subobsolete. In some taxa the lateral lobes curl up or over the central lobe, making the determination of their real size difficult. The lateral lobes vary from acute to obtuse—but their small size makes an accurate interpretation of their character difficult.

(c) *Spur*. Can be cylindrical or bifid, tapering or subclavate, straight or somewhat curved. Its size also provides a valuable character, which can usually be determined accurately on dried flowers. Only in *S. zeyheri* does this character show extensive variation.

Flower size and colour

These characters provide excellent data. Although flower size shows extensive intraspecific variation, clear interspecific patterns can be extracted. As it probably influences all other floral characters, it has frequently been used for the major division of the genus. Flower size has several measures. Floral diameter is a measurement across the open flower. For more exact purposes the length of the lateral or the dorsal sepal is used. As these differ in length, it has to be specified which one is used.

Flower colour is particularly valuable. Only three or four colours appear to exist in the genus and only white and yellow occur frequently, either singly or in combination. Only *S. cecilii* s.l. is polymorphic for colour—in other species colour can be used reliably. The inadequate and difficult to quantify colour terminology, which usually causes problems, is of no consequence here, due to the uncomplicated colour patterns and few basic colours.

TAXONOMY

Schizochilus Sond. in Linnaea **19**: 78 (1847); Bentham & Hooker, Gen. Pl. **3**: 632 (1883); H. Bol., Icones Orch. Austro-Afr. I t.18 (1893); Rolfe in Fl. Cap. **5.3**: 89 (1912); Schltr. in Beih. Bot. Centralblatt **38**: 85 (1921); Phillips, Gen. S. Afr. Fl. Pl.: 186 (1926); Schltr., Die Orchideen ed. 2: 67 (1927); Summerh. in Fl. Trop. E. Afr. **156**: 29 (1968); Senghas in Schltr., Die Orchideen ed. 3: 212 (1973); Dyer, Gen. S. Afr. Fl. Pl. **2**: 992 (1976).

Type: S. zeyheri Sond.

ETYMOLOGY

The name is derived from the Greek "schizein" = split and "cheilos" = lip. This probably refers to the three-lobed lip.

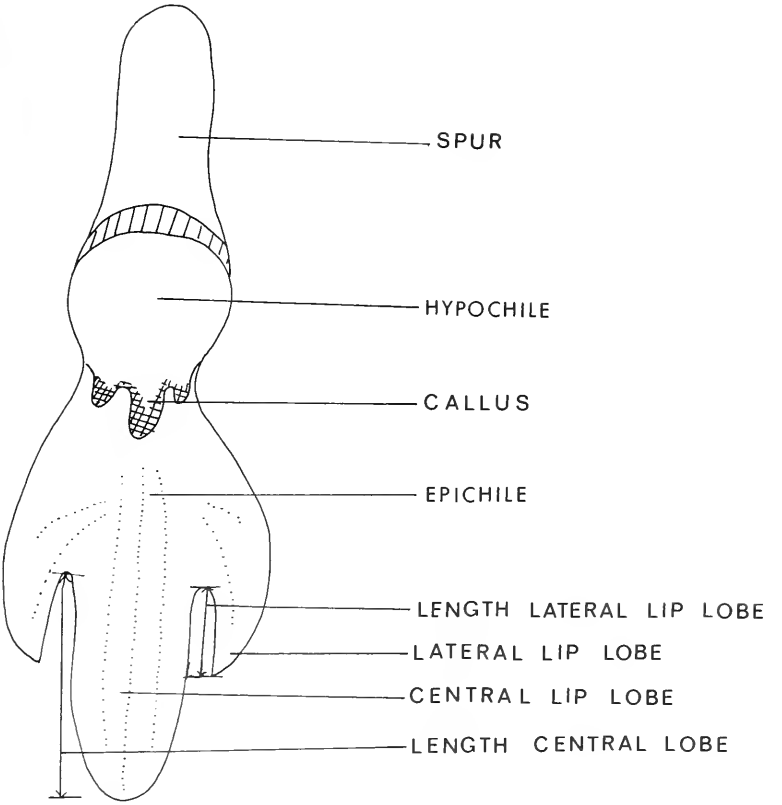

FIG. 6.
Typical lip structure in *Schizochilus*, showing the nomenclature used in this study

Essential Diagnosis

Leaves mostly linear, often clustered basally, inflorescence mostly nodding, flowers 1,5–10 mm in diameter, not resupinate; sepals subequal, lateral sepals suboblique; petals usually half as long as sepals; lip three-lobed with the lateral lobes at most half as long as the central lobe; spur 0,2–6 mm long; rostellum three-lobed with the central lobe well developed, glands naked, stigma sessile, flat.

Generic Description

Tubers testicular, cylindrico-ovate, 10–50 mm long. *Plants* slender, mostly flexuose, 50–800 mm tall; basal sheaths 1–3, hyaline or white, obtuse or acute, less than 50 mm long; leaves linear to rarely elliptic or narrowly oblanceolate or ovate, 5–30; lower leaves with a free blade 20–150 mm long, acute, semi-erect, usually the midrib prominent below; upper cauline leaves lanceolate to narrowly lanceolate, acuminate, erect, 5–30 mm long, grading into the bracts. *Inflorescence* lax to dense (mostly nodding); ovary 4–15 mm long; bracts usually acuminate, narrowly ovate to narrowly lanceolate, generally as long as the ovary, green; flowers white, white and yellow, yellow, or white with a mauve or pink tint, 1,5–10 mm in diameter. *Sepals* subequal, usually three-nerved; lateral sepals suboblique, lanceolate to ovate, 1,5–14 mm long, more or less acute; dorsal sepal usually somewhat shorter than the laterals, narrowly elliptic to broadly elliptic, or elliptic-oblong to rotund, often apiculate, shallowly galeate. *Petals* $^1/_3$–$^2/_3$ as long

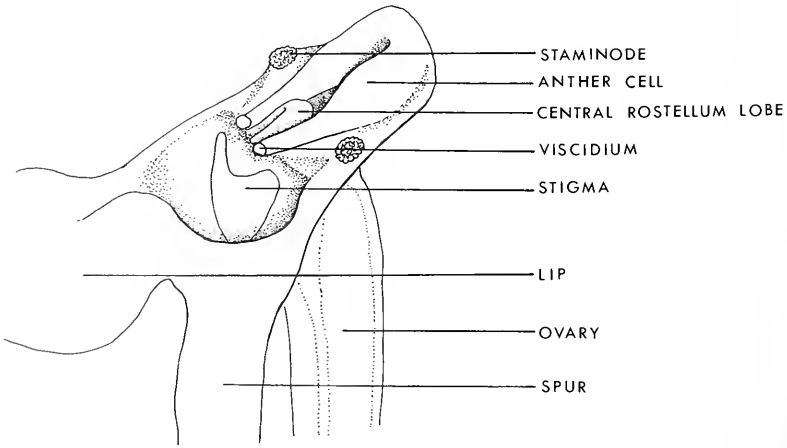

Fig. 7.
Gynostemium of *S. flexuosus* Rolfe, showing the typical structure of the rostellum

as the sepals, single-veined, oblique, usually more or less rhomboid and acute. *Lip* about as long as the sepals; the epichile more or less three-lobed, the central lobe longer than the lateral lobes; hypochile concave, leading into the spur, frequently with calli between the hypochile and the epichile; spur cylindrical to bifid, slender to clavate, always shorter than the lip, generally straight. *Rostellum* three-lobed, the central lobe a fold between the anther cells, the lateral lobes square, carrying naked viscidia. *Anther* erect or angled to 45°, 0,5–1,5 mm long. *Stigma* flat, single, borne on the column below the rostellum, above the entrance to the spur.

KEY TO THE SPECIES

1 Sepal 4 mm long or longer; spur 2–6 mm long in South Africa, 0,8–2 mm long north of Limpopo
  2 Inflorescence lax; leaves cauline
    3 Flowers bright yellow; spur rarely clavate; widespread
      4 Spur longer than 2,2 mm; from South Africa. ..... 6. **S. zeyheri**
      4′ Spur shorter than 2,2 mm; from north of Limpopo
        5 Spur 0,8–1,2 mm long; from Malawi. ..... 8. **S. sulphureus**
        5′ Spur 1,2–2,2 mm long; from the Chimanimani mountains. . . .. 7. **S. lepidus**
    3′ Flowers white or white with mauve veins; spur clavate; from the Eastern Transvaal
      6 Sepals 5–7 mm long; leaves narrowly lanceolate to linear, more than 4. ..... 9. **S. crenulatus**
      6′ Sepals 8–14 mm long; leaves elliptical, 3–5. ..... 10. **S. lilacinus**
  2′ Inflorescence dense, capitate; leaves in a basal cluster
    7 Flowers white or pinkish; lateral lip lobes subobsolete; from Ngome (Zululand). ..... 3. **S. gerrardii**
    7′ Flowers white with a yellow lip or completely yellow; lateral lip lobes ± ½ as long as the central lobe
      8 Spur shorter than 2 mm; plants from the Drakensberg at Bergville or Harrismith, above 2 200 m. ..... 4. **S. angustifolius**
      8′ Spur longer than 2,5 mm, not above localities
        9 Flowers white with a yellow lip; from Drakensberg foothills in Natal and East Griqualand. ..... 5. **S. flexuosus**
        9′ Flowers bright yellow; from Eastern Cape, as far N.E. as Maclear, rarely elsewhere. ..... 6. **S. zeyheri**

1 Sepals 4 mm long or shorter; spur 1,2–0,2 mm long in South Africa, 0,5–2 mm long in Zimbabwe
  10 Spur shorter than 0,6 mm
    11 Leaves in a basal cluster of more than 5; from the southern Drakensberg; lip without calli. ..... 2. **S. bulbinella**
    11′ Leaves cauline or not more than 3 basal, from Eastern Transvaal or Zimbabwe; lip with 3 calli
      12 Dorsal sepal less than 3 mm long; from Inyanga, Zimbabwe, flowers white or yellow. ..... 1a. **S. cecilii** ssp. **cecilii**
      12′ Dorsal sepal more than 3 mm long, from South Africa, flowers white. ..... 1b. **S. cecilii** ssp. **transvaalensis**
  10′ Spur longer than 0,6 mm
    13 Sepals less than 3,5 mm long; yellow; from Barberton and Swaziland. ..... 1c. **S. cecilii** ssp. **culveri**
    13′ Sepals more than 3,5 mm long; white; from Harrismith and Bergville. ..... 4. **S. angustifolius**

1. **Schizochilus cecilii** Rolfe in Kew Bull. **1906**: 168 (1906)

Plants subflexuose, slender, 100–300 mm tall; tubers testicular, up to 30 mm long and 10 mm in diameter; basal sheath(s) hyaline or white, 10–30 mm long, obtuse to acute; leaves 6–15; the lower 3–6 leaves clustered in the basal $^1/_5$th of the scape or basal, linear to narrowly oblanceolate, acute, semi-erect, up to 100 mm long; the remaining leaves scattered up the scape, lanceolate, acute to subacuminate, smaller towards the apex and finally grading into the floral bracts, 5–30 mm long. *Inflorescence* dense, up to 70 mm long and 10 mm in diameter, about 40-flowered; ovary ca. 4 mm long; bracts as long as or longer than the ovary, narrowly ovate to ovate, subacuminate; flowers small, ca. 2–3 mm in diameter, bright yellow or white. *Sepals* subequal, 1 or 3 veined; concave; dorsal sepal elliptic to rotund, obtuse, 2–4 mm long; lateral sepals subobliquely lanceolate to ovate, subacute, 2,5–4 mm long. *Petals* single-veined, rhomboid-rotund to ovate, acute, shallowly concave, curved over the anther, 1,3–3 mm long. *Lip* 3–3,6 mm long, 1,5–1,8 mm wide; epichile trilobed, central lobe ca. 1 mm long, lateral lobes less than half as long as the central lobe, lobes subacute; hypochile deeply concave, somewhat smaller than the epichile; disc between hypochile and epichile with three fleshy calluses; spur cylindrical, straight, 0,2–1 mm long. *Anther* curved, ca. 1 mm long.

Differential Diagnosis

This polytypic species belongs to the small-flowered group in *Schizochilus*, characterised by the sepals shorter than 4 mm and the spur shorter than 1 mm. In this group it can be distinguished from *S. bulbinella* by the presence of calli on the lip.

Biology

This species extends from Swaziland northwards along the escarpment mountains to Inyanga in Zimbabwe. Along this range it occurs in the Swaziland–Barberton mountain complex (spp. *culveri*), in the Pilgrims Rest–Lydenburg area (ssp. *transvaalensis*) and in Inyanga (ssp. *cecilii*). Over the whole range it occurs in sour secondary grassland (Acocks, 1975; Rattray, 1961). Rainfall ranges from 1 000 to 1 900 mm p.a., mostly in the summer (W.B. 29; Jackson, 1961). Mists and cloud occur frequently; snow does not occur. In this habitat it occurs in damp to well-drained grasslands, generally associated with rocky outcrops or shallow soil.

Flowering occurs from December to January and a scent has occasionally been detected. The pollination biology is unknown.

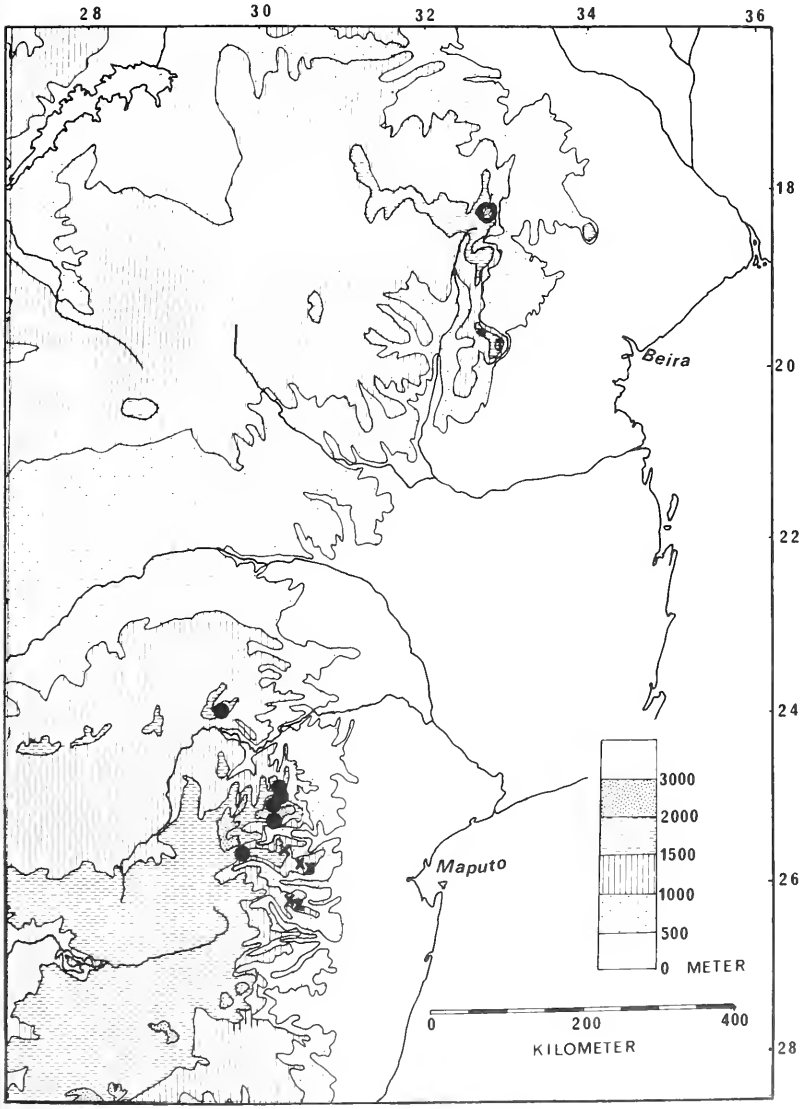

FIG. 8.
Distribution of *S. cecilii* s.l.: ○ *S. cecilii* spp. *cecilii*; ● *S. cecilii* ssp. *transvaalensis*; × *S. cecilii* ssp. *culveri*.

VARIATION

Although the three subspecies present a somewhat differing aspect, a critical analysis of the variation leaves almost no differentiating characters.

(a) Vegetative characters: *S. cecilii* ssp. *cecilii* is fairly uniform in its vegetative characters, the leaves being narrowly oblanceolate to very narrowly elliptical and somewhat rigid. In ssp. *culveri* the leaves are more linear and vary from being almost basal, to scattered on the scape. In ssp. *transvaalensis* field studies have revealed an enormous range, apparently dependent on habitat conditions. In the wetter and more densely vegetated areas, plants generally had 2–3 large leaves *(Linder 1997)*, whereas on drier drained slopes over bedrock, numerous linear leaves were produced *(Linder 2002)*. On Graskop Peak a complete range of intermediates occurred, dependent on the aspect of the slope *(Linder 1999)* (Fig. 9).

(b) Flower colour: Two states of this character occur: flowers are either yellow or white. Occasionally the white tends to cream, often the lip of the flower is cream. *S. cecilii* ssp. *culveri* always has yellow flowers. *Galpin 1144*, according to the collector's notes, had white flowers, but the flowers dried an off-white colour, indicating that they might well have been yellow. In ssp. *transvaalensis* only white or (rarely) cream flowers have been recorded, except for *Marais 318*, annotated as "bright yellow". However, in ssp. *cecilii* both colours appear. Yellow-flowered forms have been collected more frequently. *Wild 4939* notes both yellow and white flowers in the same colony. *Carley 360, Fisher 4151* and *Whellan 604* note both yellow and white flowers, with white usually rare. *Norlindh & Weimarck 4822* and *4973*, and *Beasley 37* note cream flowers.

(c) Flower size: An analysis of all available material shows that the Zimbabwean material is consistently smaller flowered than the Lydenburg material. Collections from Barberton and Swaziland are intermediate.

(d) Spur length: Material from Zimbabwe and Sabie-Lydenburg group together, with spurs less than 0,6 mm long, whereas the Barberton-Swaziland material has a spur 0,8–1 mm long.

There is thus a certain amount of variation, some of which fits the geographical patterns. As the forms occupy the same habitat over the whole range, but show some degree of morphological differentiation, they can be understood to be semi-species (Grant, 1971; White, 1978b). Formally, they are best recognised as subspecies.

a. **Schizochilus cecilii** Rolfe ssp. **cecilii**

Schizochilus cecilii Rolfe in Kew Bull. **1906**: 168(1906): Type: Rhodesia, Inyanga Mountains, 1 800–2 100 m, *Cecil 202* (K! holotype); Schltr. in Beih. Bot. Centralblatt **38**: 93 (1921).

Diagnosis

Flowers white or yellow; dorsal sepals 2–2,7 mm long, lateral sepals 2,7–3,7 mm long; spur 0,1–0,5 mm long, from Inyanga (Zimbabwe).

Representative Material

Inyanga Fort, moist soil, flowers yellow, very abundant, 31.I.1948, *Fisher 1451* in SRGH *22287* (SRGH!, NU!, K!); summit of Mt. Inyangani in rock, flowers cream, 14.II.1931, *Norlindh & Weimarck 4973* (K!).

b. **Schizochilus cecilii** Rolfe ssp. **transvaalensis** (Rolfe) Linder, comb. nov. et stat. nov.: Basionym: *Schizochilus transvaalensis* Rolfe in Fl. Cap. **5.**3: 92 (1912): Type: near Lydenburg, *Atherstone*; Mac-Mac, *Mudd* (? syntype; BOL!); Graskop, *Burtt Davy 1464* (? syntype; BOL!); Schltr. In Beih. Bot. Centralblatt **38**: 93 (1921)
? *Schizochilus tenellus* Schltr. in Beih. Bot. Centralblatt **38**: 92 (1921): Type: near Lydenburg, December 1893, *Schlechter 3934a* (B†, holotype).

Diagnosis

Flowers white or cream, very rarely yellow; dorsal sepal 2,8–3,8 mm long, lateral sepals 3,5–4,5 mm long; spur 0,2–0,6 mm long; from the Pilgrims Rest and Lydenburg areas.

Nomenclatural Notes

When Rolfe (1912) described *S. transvaalensis*, he did not indicate how he separated it from *S. cecilii*, which he had described six years before. Schlechter (1921) confessed that he had not seen any material of *S. cecilii* or *S. transvaalensis*, and based his decisions on Rolfe's descriptions. He noted that *S. cecilii* and *S. transvaalensis* appear to be very similar, but that *S. transvaalensis* has larger flowers. He also noted the affinity between these two taxa and *S. culveri*. He did not note the affinity between these taxa and *S. tenellus*, which he placed near *S. gerrardii*. I have not seen the type of *S. tenellus* but from the description it is likely to be the same as *S. cecilii* ssp. *transvaalensis*.

Representative Material

Pilgrims Rest near Graskop at Gods Window, flowers white, in damp grassland, 4.I.1979, *Linder 1997* (BOL!, PRE!, K!); Lydenburg, near summit of Long Tom Pass, flowers white, in shallow soil; 5.I.1979, *Linder 2002* (BOL!, PRE!, K!)

c. **Schizochilus cecilii** Rolfe ssp. **culveri** (Schltr.) Linder, comb. nov. et stat. nov.: Basionym: *Schizochilus culveri* Schltr. in Beih. Bot. Centralblatt **38**: 90 (1921): Type: Barberton, Little Lomati Valley, *Culver 76* (B†, holotype; BOL!).

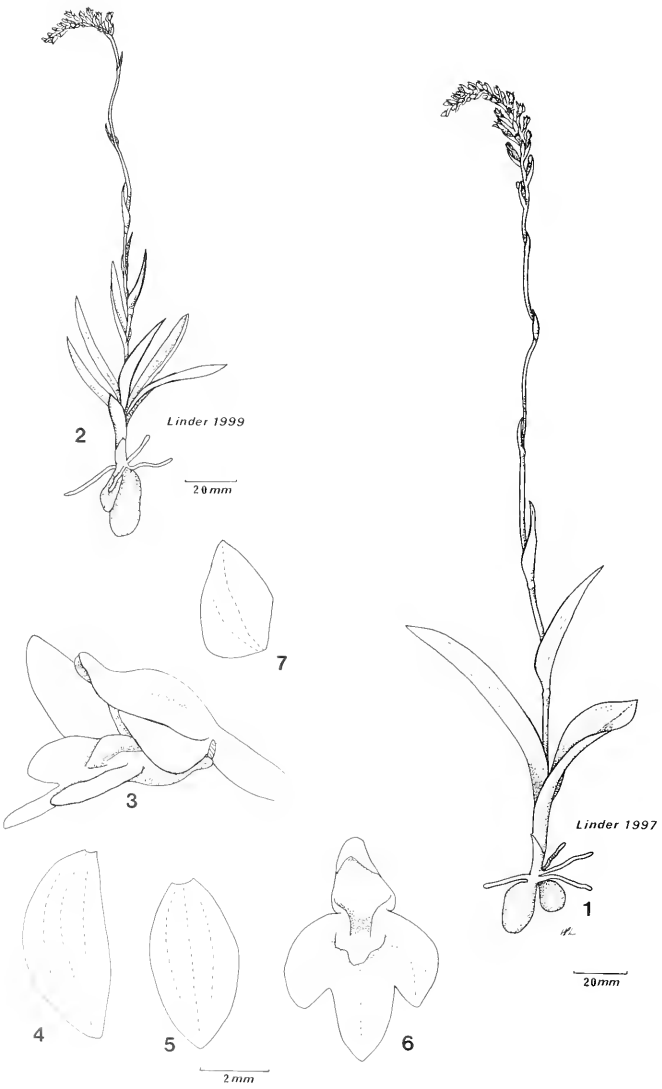

FIG. 9.
S. cecilii ssp. *transvaalensis*. 1. *Linder 1997* from damp conditions near Gods Window, whole plant. 2. *Linder 1999* from dry conditions on Graskop Peak, whole plant. 3 to 7 based on *Linder 1999:* 3. Side view of flower with the lateral sepal removed. 4. Lateral sepal. 5. Dorsal sepal. 6. Lip. 7. Petal.

Schizochilus galpinii Schltr. in Beih. Bot. Centralblatt **38**: 92 (1921): Type: Swaziland, mountaintops at Horo Concession, December 1890, *Galpin 1144* (B†, holotype; BOL!, PRE!).
Schizochilus bulbinella auct. non (Reichb.f.) H.Bol.: Rolfe (1912) pro parte; Compton, Fl. Swaziland: 156 (1976).

Diagnosis

Flowes yellow; sepals 2,5–3,5 mm long, spur 0,8–1 mm long; in mountains between Barberton and Mbabane.

Nomenclatural Notes

Rolfe included *Galpin 713* in *S. bulbinella*—Schlechter noted that this collection could be separated on the basis of the lip shape, and the presence of lip calli, and described it as *S. culveri*. In the same publication he described *S. galpinii*, which differs mainly in having white flowers. Analysis of isotype material has revealed no other differences from the type of *S. culveri*. The concept of *S. culveri* was still not clear, and in 1976 Compton mistook material of *S. culveri* for *S. bulbinella*.

Representative Material

Barberton, Bosch's, flowers bright golden yellow, XI.1889, *Galpin 713* (BOL!, GRA!); Mbabane, Nduma, in rock crevices, flower bright yellow, 19.I.1956, *Compton 25382* (PRE!).

2. **Schizochilus bulbinella** (Reichb.f.) H.Bol. in Jl. Linn. Soc. **25**: 205 (1889); Dur. & Schinz, Consp. Fl. Afr. **5**: 116 (1894); Rolfe in Fl. Cap. **5**.3: 93 (1912); Schltr. in Beih. Bot. Centralblatt **38**: 89 (1921); Jacot Guillarmod, Fl. Lesotho: 157 (1971); Ross, Fl. Natal: 142 (1972).
Brachycorythis bulbinella Reichb.f. in Flora **1867**: 116 (1867): Type: Fakus District, *Dr Sutherland* (? holotype).
Platanthera bulbinella (Reichb.f.) Schltr. in Bot. Jahrb. 20 Beih. **50**: 12 (1895).
Gymnadenia bulbinella (Reichb.f.) Kraenzl. in Orch. Gen Sp. **1**: 561 (1898).
Schizochilus burchellii Jackson in Ind. Kew. Suppl. **1**: 384 (1906) (nom. nud.).

Plants slender, subflexuose, 80–250 mm tall; tubers testicular, 20–40 mm long, ca. 10 mm in diameter; basal sheaths several, obtuse to acute, hyaline to white, 20–40 mm long; leaves 10–30, the lower 4–20 basal, semi-erect, 30–50–100 mm long, usually all the same length, 2–5–9–(14) mm wide, acute, somewhat conduplicate, very narrowly oblanceolate with the midrib prominent below, the upper 5–10 leaves scattered on the scape, acute to subacuminate, 5–20 mm

long, 2–4 mm wide, grading into the floral bracts. *Inflorescence* dense, generally oblong cylindrical, 20–40 mm long, ca. 10 mm in diameter; ovary 3–4 mm long; bracts as long as or somewhat longer than the ovary, narrowly ovate, acuminate; flowers small, ca. 3 mm in diameter, bright yellow. *Sepals* subequal, three-nerved; dorsal sepal very broadly obovate to rotund, apiculate, deeply galeate, 2,5–3 mm long; lateral sepals obliquely narrowly ovate, subacute, shallowly keeled, 2,5–3,5 mm long. *Petals* single-veined, suboblique, broadly ovate, obtuse, shallowly concave and curved over the anther, 1,5–2 mm long. *Lip* 3–4 mm long, 1–2 mm wide; epichile trilobed, central lobe ca. 1 mm long, lateral lobes ca. 0,3 mm long or smaller, curved over the central lobe; hypochile much smaller than the epichile, deeply concave, no calli present; spur cylindrical, obtuse, ca. 0,3 mm long. *Anther* erect, ca. 0,8 mm long.

Differential Diagnosis

The small (sepals 2,5–3,5 mm long) flowers place this species in the small-flowered group. It is unique in this group by the absence of calli, dense cluster of basal leaves and relatively small lateral lip lobes and the narrow lip. It is geographically isolated in the southern Drakensberg from the other small-flowered taxa.

Variation

This species shows little variation, except in the width and number of basal leaves. These two characters have been found to vary within one population.

Biology

S. bulbinella is restricted to the Drakensberg and its outliers between Underberg and Maclear. The altitudinal range is from 1 500 m to 2 500 m above sea-level. Acocks (1975) described this veld type as "Highland Sourveld". Killick (1963) placed it in the "Subalpine Belt". Both grassland and proteoid savanna occur in this vegetation type. Precipitation ranges from 750–1 200 mm p.a., mostly in summer, with snow-falls in the winter (W.B. 29).

All the populations studied were in shallow (10–100 mm) soil over rock, usually in slightly damp to dry situations, never in wet places. Most of the populations were on Cave Sandstone, but the species has been recorded from Basalt and Dolerite. The habitat comparative to the other species of *Schizochilus* in Natal is indicated in Figure 2.

Populations tend to be large, with 50–200 plants, frequently growing sociably. Within its distribution range this species is by no means rare.

Hilliard and Burtt 8927 indicate a scent, but this is the only record; the author could not detect one. Although copious seed-set has been observed, the pollination biology is unknown. Flowering occurs during January and February.

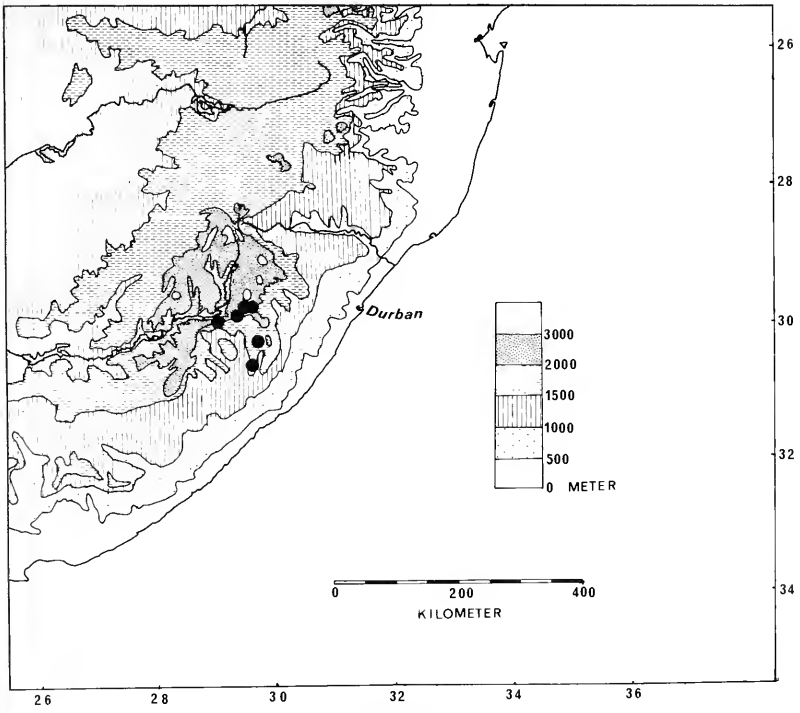

FIG. 10.
Distribution of *S. bulbinella* (Reichb. f.) H. Bol.

NOMENCLATURAL NOTES

The type collection is from Fakus District, in East Griqualand. The only synonym is the *nomen nudum* described—probably by accident—in *Index Kewensis*.

REPRESENTATIVE COLLECTIONS

Mt. Curry, 1 950 m. II.1883, *Tyson 1072* (BOL!, GRA!); Ramatseliso, stony plateau, flowers yellow, common, 30.I.1977, *Boardman 239* (PRE!); Underberg, Bushmansnek, 2 400 m, flowers deep yellow, fragrant, on stony places, 4.II.1976, *Hilliard & Burtt 8927* (NU!).

3. **Schizochilus gerrardii** (Reichb.f.) H.Bol. in Jl. Linn. Soc. **25**: 205 (1889); Dur. & Schinz, Consp. Fl. Afr. **5**: 116 (18923; Rolfe in Fl. Cap. **5**.3: 94 (1912); Schltr. in Beih. Bot. Centralblatt **38**: 91 (1921).
Brachycorythis gerrardii Reichb.f. in Flora **1867**: 116 (1867): Type: Ingoma, *Gerrard 1542* (TCD!, holotype).
Platanthera gerrardii (Reichb.f.) Schltr. in Bot. Jahrb. **20** Beih. **50**: 12 (1895).
Gymnadenia gerrardii (Reichb.f.) Kraenzl. in Orch. Gen. Sp. **1**: 562 (1898).

Plant slender, often subflexuose, 150–300 mm tall; tubers testicular, up to 40 mm long and 20 mm in diameter; outer basal sheath hyaline with brown veins, obtuse, ca. 20 mm long; inner sheath white, acute to apiculate; leaves up to 25; the lower 6–10 leaves basal, linear, acute to subacuminate, semi-erect, up to 110 mm long and 10 mm wide, usually 70 mm long and 5 mm wide; the remaining leaves more or less narrowly ovate, erect, sheathing, scattered up the scape, basally up to 60 mm long, apically grading into the floral bract. *Inflorescence* dense, cylindrical, up to 50 mm long and ca. 15 mm in diameter, ca. 50 flowered; ovary ca. 5 mm long; bracts longer towards the base of the spike, overtopping the flowers, narrowly ovate, acuminate; flowers 5–8 mm in diameter, white suffused with pink or mauve, veins on sepals mauve, lip with a greenish spot on the disc. *Sepals* three-nerved, subequal; dorsal sepal narrowly elliptic to elliptic, concave, acute to apiculate, 5–7,5 mm long; lateral sepals suboblique, lanceolate to narrowly ovate, shallowly keeled, acute, 5–8 mm long. *Petals* one-nerved, obliquely rhomboid-ovate, acute, 2,5–3 mm long. *Lip* 4–6 mm long, 2 mm wide, epichile obscurely tri-lobed, lobes acute, central lobe ca. 1 mm long, lateral lobes 0,1–0,2 mm long; lateral lobes upcurved; hypochile concave, smaller than the epichile; disc between hypochile and epichile with three calli; spur cylindrical, obtuse, straight, ca. 1 mm long. *Anther* erect, ca. 1 mm tall.

Differential Diagnosis

This species belongs in the large-flowered group, with sepals longer than 4 mm. In this group, the almost obsolete lateral lip lobes and the green disc are unique. The basally clustered leaves separate it from most of the *S. zeyheri* group. It is the only species of *Schizochilus* occurring on the Ngome Highlands in Zululand.

Variation

Although this species occupies such a small area, extensive inter-population variation in flower colour, flower size and tepal shape occurs. Populations at the extremes of the distribution range (*Linder 1953, 1960*) have smaller flowers with wider sepals, than populations near the centre of the range (i.e. *Linder 1957*). Flower colour showed a gradient from almost pure white flowers (*Linder 1953*, at

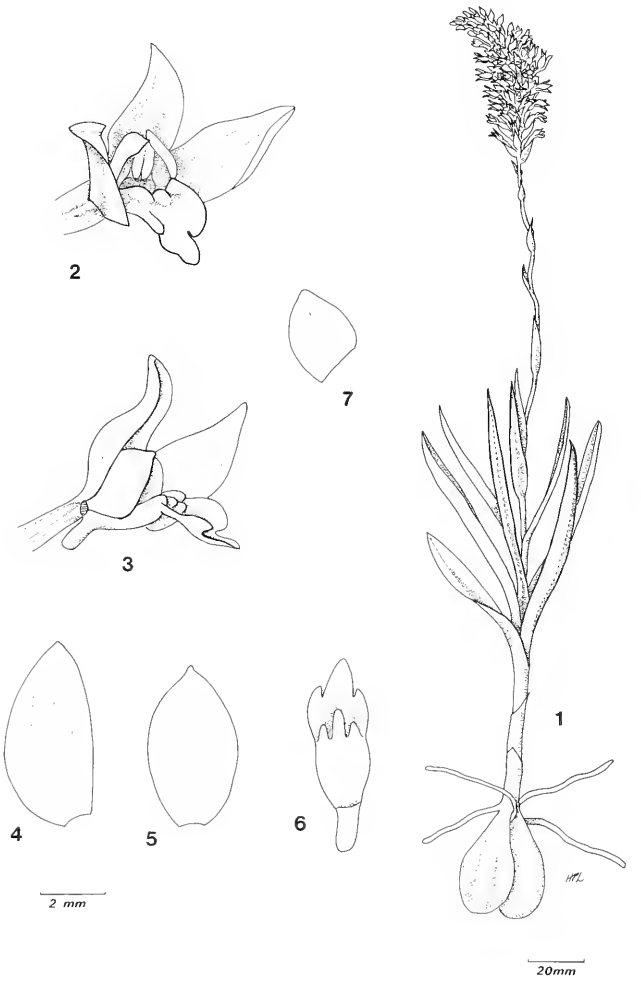

FIG. 11.
S. gerrardii (Reichb. f.) H. Bol., from *Linder 1960*. 1. Whole plant. 2. Flower, front view. 3. Flower with lateral sepal removed, side view. 4. Lateral sepal. 5. Dorsal sepal. 6. Lip. 7. Petal.

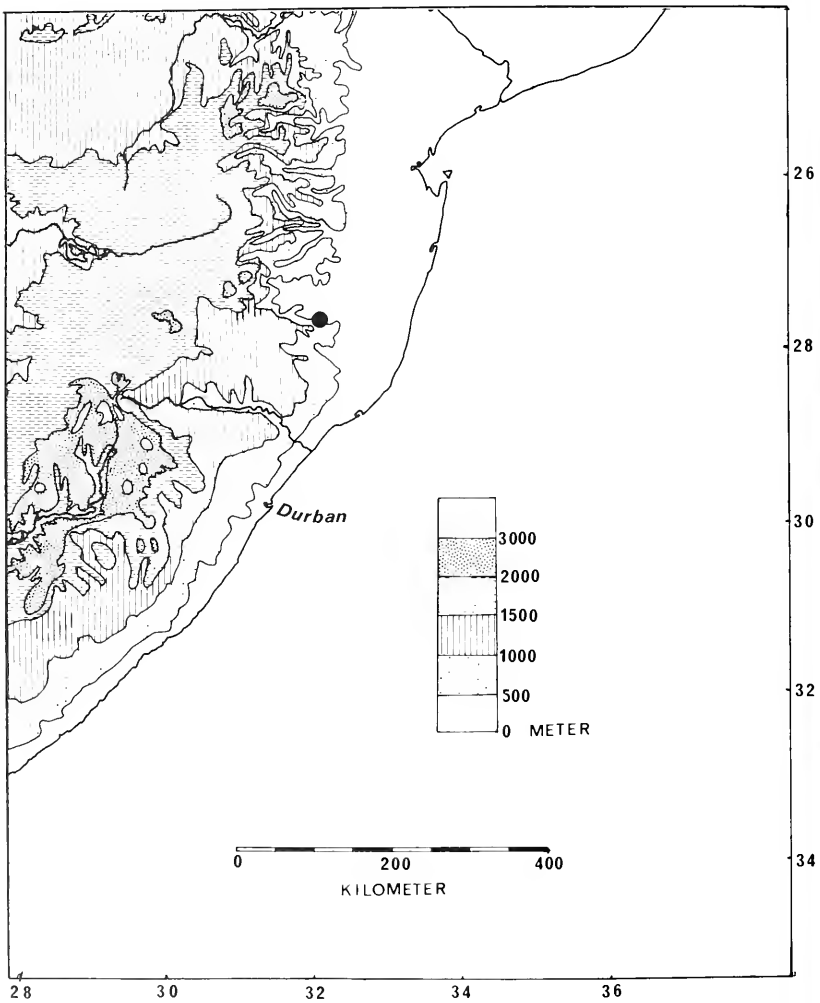

FIG. 12.
Distribution of *S. gerrardii* (Reichb. f.) H. Bol.

the eastern end of the range) through flowers somewhat suffused with pink, with darker pink veins, in the centre of the range (*Linder 1957*) to flowers all deeply suffused with pink at the western end of the range (*Linder 1960*).

Biology

Schizochilus gerrardii appears to be restricted to the Ngome and Ceza Highlands (3127 CD) on the spur between the Mkuze and Black Umfolozi Rivers, at an altitude of ca. 1 200 m. Acocks (1975) mapped the area as Veld type 8: North-eastern Mountain Sourveld, a very sour secondary grassland dominated by *Themeda triandra*. Bayer (1938) mentions the existence of a "grassland formation" in this area. The rainfall in the area is about 1 600 mm (W.B. 29), of which 82 % falls in summer.

S. gerrardii occurs around the margins of outcropping bedrock in shallow soil. Frequently there are slight seepages. Only rarely do isolated plants occur in grassland. It is a sociable species, and usually locally abundant. Plants often form dense clusters. Although this species is thus relatively common in its habitat, the extension of the *Pinus patula* plantations could drastically reduce the total number of existing populations.

There is no record of any scent, and nothing is known about the pollination biology of this species. Copious seed-set was observed. Flowering occurs from December to February.

Nomenclatural Notes

Until recently, this species was only known from the type collection. Rolfe extended the species concept to include material from *S. cecilii* ssp. *transvaalensis (Wilms 1385)* and from *S. flexuosus* Rolfe *(Schlechter 6477, Krook* in Herb. Penther *660).* Schlechter understood the species as defined here. Ross (1972) however, followed Rolfe (1912), and cited *Schlechter 6477* as material of *S. gerrardii*, and he gives the distribution range of *S. gerrardii*, as understood by him, as Natal Uplands. However, this species is restricted to Zululand. The treatment of Ross thus has to be understood as a misidentification.

Representative Material

Zululand, Natal, Ngome, 1.I.1979, *Linder 1957* (BOL, PRE, NU, K); Zululand, Ngome, near sawmill, 7.XII.1975, *Hilliard & Burtt 8418* (NU).

4. **Schizochilus angustifolius** Rolfe in Fl. Cap. **5.**3: 93 (1912): Type: Van Reenen, 1 500–1 800 m, *Wood 3444* (K, lectotype; BOL!); Ross, Fl. Natal: 142 (1972).
Schizochilus albiflos Schltr. in Beih. Bot. Centralblatt **38:** 91 (1921) : Type: Mount Aux Sources, *Wood s.n.* (B†, holotype; SAM!, NBG!, GRA!).

Plants slender, subflexuose, 50–200 mm tall; tubers testicular, ca. 15 mm long, 10 mm in diameter; basal sheath hyaline acute; leaves 7–14; about $^2/_3$ of the leaves in a basal cluster, linear to narrowly oblanceolate, semi-erect, shallowly keeled, acute, 30 to 60 mm long; the remainder scattered on the scape, grading from the basal leaves into the floral bracts, more or less acuminate. *Inflorescence* dense, cylindrical-oblong, up to 40 mm long and 10 mm in diameter; ovary ca. 4 mm long; bracts as long as the ovary, narrowly ovate, acuminate; flowers 2–3 mm in diameter, sepals and petals white, lip yellow. *Sepals* subequal, tri-nerved; 4–5 mm long; dorsal sepal broadly elliptic, galeate, apiculate; lateral sepals subobblique, narrowly ovate to ovate, shallowly keeled, obtuse to acute. *Petals* single-nerved, ovate, acute, ca. 2 mm long. *Lip* 3,5–5 mm long, epichile broadly three-lobed, central lobe ca. 1,5 mm long, lateral lobes 0,8 mm long, all acute; hypochile much smaller than the epichile, concave, no calli present; ca. 3 mm wide; spur obtuse, ca. 1 mm long. *Anther* erect, ca. 1 mm tall.

Differential Diagnosis

S. angustifolius is intermediate between the small-flowered and large-flowered groups. The yellow and white flowers and the sepal length of 4–5 mm, distinguish it from the small-flowered group. From the South African representatives of the large-flowered group it can be separated by the short spur (1 mm long), and from *S. gerrardii* by the smaller flowers. It is the only species of *Schizochilus* occurring in basalt in the Northern Natal Drakensberg.

Biology

This species appears to be restricted to altitudes between 2 100 m and 3 000 m in the Drakensberg between Giant's Castle and Harrismith Platberg. Acocks (1975) termed the vegetation in this zone as Veld type 58: *Themeda-Festuca* Alpine veld. He describes it as a short dense grassland on black turfy soils. West (1951) and Herbst and Roberts (1974) term the vegetation as alpine, whereas Killick (1963, 1978) defines it as sub-alpine. Herbst and Roberts (1974) indicate a rainfall of ca. 1 270 mm, and a temperature range of 22 °C to −13 °C. Snow occurs frequently in winter, and the rainfall is almost entirely in summer.

The habitat is usually described as being "between stones", but I have found this species growing in grassland, on steep bare banks above old footpaths, in slightly damp localities. The single population studied was fairly extensive, but the plants showed little sociability. No estimates of the number of populations is possible—the area has not been extensively investigated.

No scent has been recorded, and although copious seed-set was observed, the pollination biology of this species is unknown. Flowering occurs in January and February.

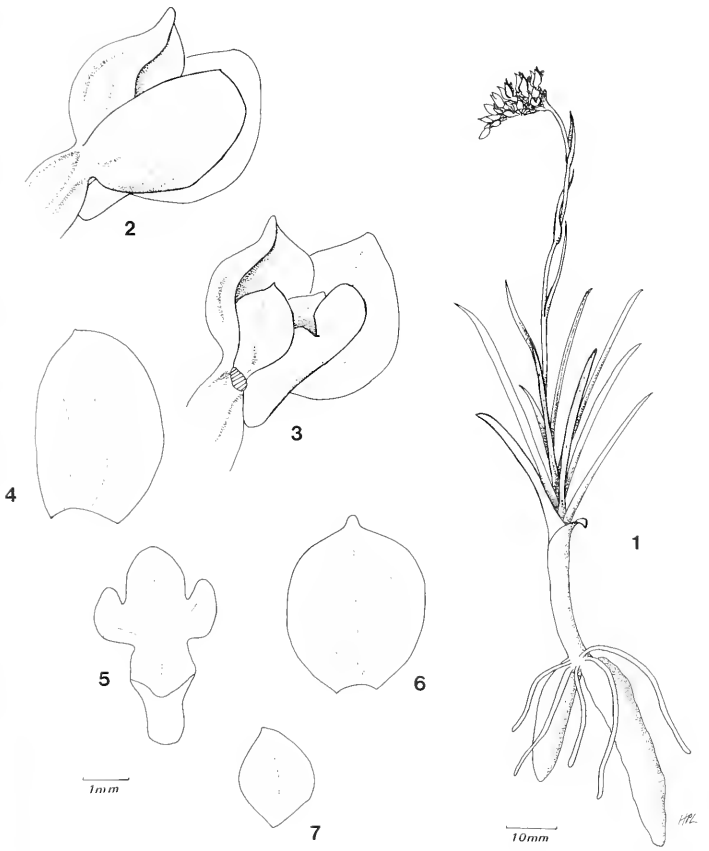

FIG. 13.
S. angustifolius Rolfe. 1. Whole plant, from *Jacobsz 2523*. 2 to 7 from *Linder 2077*. 2. Side view of flower. 3. Side view of flower with lateral sepal removed. 4. Lateral sepal. 5. Lip. 6. Dorsal sepal. 7. Petal.

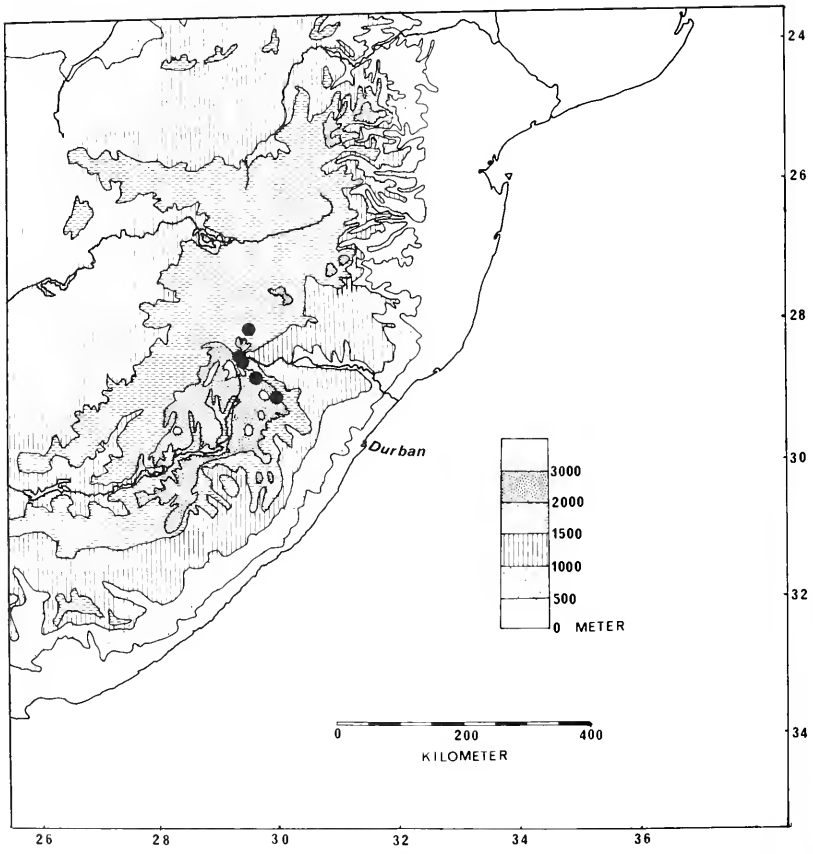

FIG. 14.
Distribution of *S. angustifolius* Rolfe

NOMENCLATURAL NOTES

Rolfe based his species on *Sankey 256, Wood 3444, Allison 6* and *Schlechter 6484*. Of these, the first three collections agree with the concept of this species as understood here; *Schlechter 6484* has to be included in *S. flexuosus* Rolfe. In 1921 Schlechter, pointing out that *S. angustifolius* was based on a mixed type, lectotypified *Schlechter 6484*—as a reason he stated that the description fits this collection best. For the remaining collections he proposed the name *S. albiflos*,

with *Wood s.n.* (Van Reenen) as type. A careful comparison of both *Schlechter 6484* and *Wood 3444* with Rolfe's description shows that the description agrees more with *Wood 3444* than with *Schlechter 6484* (See Table 1). Rolfe's key determines *Wood 3444* as *S. angustifolius* and *Schlechter 6484* as *S. flexuosus*. According to Article 8 of the I.C.B.N. (1978): "The author who first designates a lectotype or a neotype must be followed, . . . it may be superseded if it can be shown that the choice was based upon a misinterpretation of the protologue . . .". In this case, as the protologue does not agree with *Schlechter 6484, Wood 3444* is proposed as the lectotype of *S. angustifolius* Rolfe, and *S. albiflos* sensu Schltr. is reduced to the synonymy of *S. flexuosus* Rolfe.

TABLE 1

Comparison of *Wood 3444* (BOL) and *Schlechter 6484* (BOL) with the protologue of *S. angustifolius* Rolfe.

Protologue	*Wood 3444*	*Schlechter 6468*
1. "Sepals over $^1/_6$" (4 mm) long"	Sepals 4 mm long	Sepals 8 mm long
2. "Sepals ovate or ovate-oblong"	Sepals narrowly ovate or ovate	Sepals lanceolate
3. "Lip . . . side lobes . . . obtuse"	Lip side lobes obtuse	Lip side lobes acute
4. "Spur . . . one quarter as long as limb" (=lip)	Spur 0,8 mm long, lip 3 mm long.	Spur 3 mm long, lip 7 mm long.

REPRESENTATIVE MATERIAL

Harrismith Platberg, 2 425 m, between rocks, flowers white and yellow, 10.I.1974, *Jacobsz 2523* (PRE); Bergville, Royal Natal National Park, Witzieshoek car park, 22.I.1977, *Stewart 1949* (NU); Cathedral Peak, 18.I.1965, *Schelpe 7199* (BOL).

5. **Schizochilus flexuosus** Harv. ex Rolfe in Fl. Cap. **5.**3: 92 (1912): Type: Liddesdale, *Fannin 56* (TCD!, holotype); Schltr. in Beih. Bot. Centralblatt **38**: 97 (1921); Ross, Fl. Natal: 142 (1972).
Schizochilus pulchellus Schltr. in Beih. Bot. Centralblatt **38**: 93 (1921): Type: Mt. Insiswa, January 1895, *Schlechter 6477* (B†, holotype; BOL!, PRE!, GRA!).
Schizochilus angustifolius Rolfe emend. Schltr. in Beih. Bot. Centralblatt **38**: 97 (1921): Lectotype: Mt. Insiswa, January 1895, *Schlechter 6484* (B†, holotype; BOL!).
Schizochilus baurii Schltr. in Beih. Bot. Centralblatt **38**: 99 (1921): Type: Mt. Bazija, 1 200 m, February, *Baur 630* (B†, holotype; BOL!, SAM!).

Plants slender, subflexuose, 50–250 mm tall; tubers testicular, 10–20 mm long, 7 mm in diameter; basal sheaths hyaline, obtuse, up to 20 mm long; leaves 10–30; the lower 6–20 basal, usually all the same length, linear to oblanceolate, semi-erect, flat to keeled, acute or shortly apiculate, 20–50 mm long, 2–8 mm wide; cauline leaves scattered on the scape, mostly narrowly lanceolate, acuminate, grading from the basal leaves into the floral bracts. *Inflorescence* dense, usually subcapitate, 20–40 mm long, 5–20–(30) flowered; ovary ca. 5 mm long; bracts as long as or longer than the ovary, narrowly ovate, acuminate, shallowly keeled; flowers large, ca. 5 mm in diameter, the sepals and petals white, the lip yellow. *Sepals* three-nerved, subequal; dorsal sepal galeate, elliptic, apiculate, 5–7 mm long; lateral sepals shallowly keeled, suboblique, lanceolate to narrowly ovate, acute, 6–9 mm long. *Petals* single-nerved, suboblique, narrowly ovate-rhomboid to lanceolate rhomboid, acute, 2,5–4,5 mm long. *Lip* 4–8 mm long, 3–4 mm wide; epichile deeply three-lobed, the central lobe ca. 2 mm long, the lateral lobes about half as long, lobes acute; hypochile much smaller than the epichile, disc calli rudimentary or absent; spur subcylindrical, subclavate, somewhat pendent, 3–4 mm long. *Anther* erect or somewhat angled, ca. 1,5 mm long.

Differential Diagnosis

This species is very closely allied to *S. zeyheri*, from which it can be separated by the white sepals. In the geographic overlap zone it may also be distinguished by the capitate inflorescences and basally clustered leaves. The floral structure distinguishes this group from the rest of the genus.

Variation

There is little variation that can be correlated to geography. Flower size and robustness vary, and depauperate specimens can have very few flowered, almost lax-looking inflorescences, associated with rather weakly developed basal leaves. *Devenish 853*, from Utrecht appears to be intermediate to *S. zeyheri*, with which it co-occurs. Flower colour is as for *S. flexuosus*, but the leaves and spur dimensions agree more with *S. zeyheri*.

Biology

S. flexuosus is restricted to the foothills and outliers of the Drakensberg between Maclear in the Eastern Cape, and Bergville in Natal, except for one collection from Ermelo in the Transvaal *(v.d. Merwe 1122)* and from Utrecht *(Devenish 853)*. In this area it occurs between 1 500 and 2 500 m above mean sea level. Acocks (1975) described the vegetation of this zone as Veld type 44: Highland Sourveld. It is essentially a tussocked grassland, and occasionally a proteoid savanna (West, 1951; Adamson, 1938; Killick, 1963). The rainfall in this area ranges from 1 000 mm to 1 300 mm p.a., mostly in the summer, with

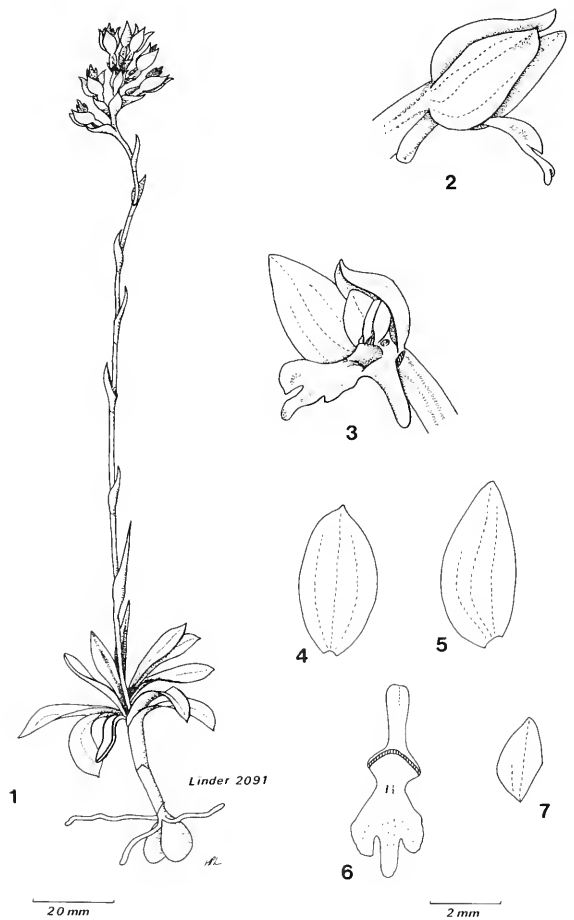

FIG. 15.
S. flexuosus Rolfe, from *Linder 2091*. 1. Whole plant. 2. Side view of flower. 3. Side view of flower with the lateral sepal removed. 4. Dorsal sepal. 5. Lateral sepal. 6. Lip. 7. Petal.

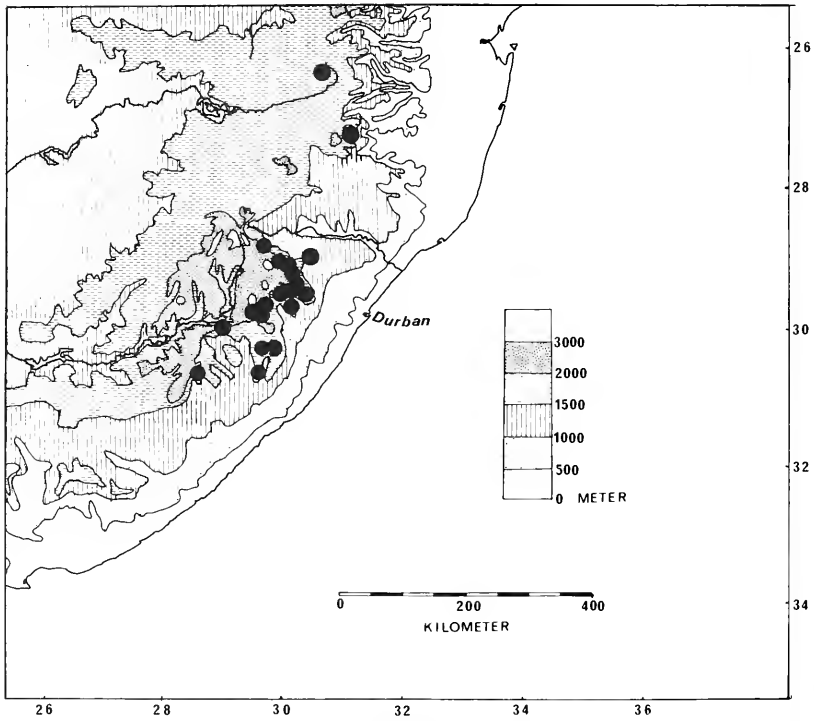

FIG. 16.
Distribution of *S. flexuosus* Rolfe

frequent snow in the winter (W.B. 29). Mists occur frequently. The substrate is usually Cave Sandstone, rarely Dolerite.

In this habitat *S. flexuosus* occupies damp grassland, often in shallow soil over bedrock. For a comparison of its habitat with that of other species of *Schizochilus*, see Figure 2. Populations are usually not very large, but the species appears to be fairly common. Scent faint, sweetish. Pollination biology is unknown. Flowering occurs in January and February.

NOMENCLATURAL NOTES

S. flexuosus was described in 1912 by Rolfe, from material housed at TCD. In 1921 Schlechter described three more taxa in this group—he had not seen any material of *S. flexuosus* Rolfe.

Baur 630, on which Schlechter based *S. baurii*, had been determined by Rolfe (1912) as *S. zeyheri*. Schlechter pointed out that his *S. baurii* was more closely related to *S. flexuosus* Rolfe than to *S. zeyheri*, but separated it on having larger flowers and differently shaped petals—both characters which are highly variable in *S. flexuosus*. *S. pulchellus*, based on material determined by Rolfe to be *S. gerrardii* appears to be a rather depauperate specimen of *S. flexuosus*. It has peculiarly narrow floral segments. Schlechter did not appreciate its affinity to *S. flexuosus*. *S. angustifolius* Rolfe emend. Schlechter is discussed above.

Representative Collections

Kokstad, I.1884, *Tyson 1600* (SAM!, GRA!, BOL!); Natal, Bushmans Nek, 2 750 m, 2.II.1976, *Hilliard & Burtt 9021* (NU!); Bulwer, Natal, Marawaga Mt., 2 100 m, 31.I.1957, *Marais 1454* (PRE!).

6. **Schizochilus zeyheri** Sond. in Linnaea **19**: 78 (1847): Type: Winterberg Range, *Ecklon & Zeyher s.n.* (S!, holotype); H. Bol. in Jl. Linn. Soc. **25**: 205 (1889); Dur. & Schinz, Consp. Fl. Afr. **5**: 116 (1892); H. Bol., Icones Orch. Austro-Afr. **1** t.18 (1893); Rolfe in Fl. Cap. **5**.3: 90 (1912); Schltr. in Beih. Bot. Centralblatt **38**: 97 (1912); Ross, Fl. Natal: 142 (1972).
Brachycorythis zeyheri (Sond.) Reichb.f. in Flora **1867**: 117 (1867).
Platanthera zeyheri (Sond.) Schltr. in Bot. Jahrb. **20** Beih. **50**: 12 (1895).
Gymnadenia zeyheri (Sond.) Kraenzl., Orch. Gen. Sp. **1**: 561 (1898).
Schizochilus sandersonii Harv. ex Rolfe in Fl. Cap. **5**.3: 91 (1912): Type: Fields Hill, Natal, *Sanderson 564* (TCD!, syntype); near Durban, *Gerrard 2176* (TCD!, syntype); Inanda, *Wood 478* (? syntype, BOL!, SAM!); Schltr. in Beih. Bot. Centralblatt **38**: 98 (1921); Ross, Fl. Natal: 142 (1972).
Schizochilus strictus Rolfe in Fl. Cap. **5**.3: 91 (1912): Type: Klein Olifantsriver, *Schlechter 4028* (K!, syntype; PRE!, BOL!, GRA!); Lydenburg, O'Neills Farm, *Wilms 1397* (K!, syntype); Schltr. in Beih. Bot. Centralblatt **38**: 96 (1921); Dyer, Fl. Pl. S. Afr. **24** t.941 (1944); Ross, Fl. Natal: 142 (1972); Compton, Fl. Swaziland: 156 (1976).
Schizochilus trilobus Rolfe in Fl. Cap. **5**.3: 91 (1912): Type: Dargle Farm, *Fannin 8* (TCD!, holotype); Schltr. in Beih. Bot. Centralblatt **38**: 99 (1921); Ross, Fl. Natal: 142 (1972).
Schizochilus rehmannii Rolfe in Fl. Cap. **5**.3: 92 (1913): Type: Houtbosch, *Rehmann 5849* (? syntype); Lydenburg, Atherstone (? syntype; GRA!, SAM!) Mac Mac, *Mudd* (? syntype); Schltr. in Beih. Bot. Centralblatt **38**: 100 (1921).
Schizochilus caffrus Schltr. in Beih. Bot. Centralblatt **38**: 94 (1921): Type: Bazijaberg 1 200 m, February, *Baur 631* (B†, holotype; NBG).
Schizochilus bolusii Schltr. in Beih. Bot. Centralblatt **38**: 95 (1921): Type: Swaziland, highveld between Mbabane and Oshoek, Jan. 1906, *Bolus 12321* (B†, holotype; BOL!, PRE!).

Schizochilus rudatisii Schltr. in Beih. Bot. Centralblatt **38**: 95 (1921): Type: Natal, Alexandra County, Fairfield, November 1905, *Rudatis 159* (B†, holotype).
Schizochilus clavatus Schltr. in Beih. Bot. Centralblatt **38**: 96 (1921). Type: Elandspruitbergen, December 1893, *Schlechter 3989* (B†, syntype); Belfast, February 1909, *Doidge 551* (B†, syntype).
Schizochilus huttonae Schltr. in Beih. Bot. Centralblatt **38**: 99 (1921): Type: ? Johannesburg, *Hutton 275* (B†, holotype; GRA!, PRE!).
Schizochilus woodii Schltr. in Beih. Bot. Centralblatt **38**: 99 (1921): Type: Van Reenen, 5 000–6 000′, February 1904, *Wood 9307* (B†, holotype; NBG!).
Schizochilus grandiflorus Schltr. in Beih. Bot. Centralblatt **38**: 100 (1921): Type: Swamps and streams at Dokin, *Bachmann 416* (B†, holotype).
Schizochilus grandiflorus Schltr. var. *crenulatus* in Beih. Bot. Centralblatt **38**: 101 (1921): Type: Umkwani, *Tyson 2605* (B†, syntype; PRE!, SAM!, GRA!) Port St. Johns, *Galpin 3416* (B†, syntype; BOL!, PRE!).

Plants slender, rarely subflexuose, 150 to 600 mm tall; tubers testicular, 10–40 mm long; basal sheaths 1–3, hyaline or white, acute to obtuse; leaves 5–18; the lower 3 to 10 linear to very narrowly elliptical, basal or spread on the lower half of the scape, 40–140 mm long, 3–10–(17) mm wide, acute, semi-erect; the upper leaves lanceolate acuminate sheaths, grading into the floral bracts. *Inflorescence* lax, rarely dense, subcapitate, up to 100 mm long, and up to 30 flowered; ovary 5–10 mm long; bracts about as long as ovary, lanceolate, acuminate; flowers 4–6 mm in diameter, bright yellow, lip a richer yellow than the sepals. *Sepals* subequal, three-veined; acute; dorsal sepal subgaleate, narrowly elliptical, rarely apiculate, 4,5–11 mm long; lateral sepals somewhat larger, shallowly keeled, oblique, lanceolate, 4,5–11 mm long. *Petals* single-veined, flat or shallowly concave, suboblique, ovate to lanceolate, acute to subacuminate, 2,5–6 mm long. *Lip* 6–12 mm long, 4–6 mm wide; epichile deeply three-lobed, lobes narrowly ovate, very acute, central lobe up to 2 mm long, lateral lobes ca. 1 mm long; hypochile concave, much smaller than epichile; disc with three fleshy calli; spur straight, cylindrical, rarely subovate or subbifid or tapering; 2–6 mm long. *Anther* erect or angled, ca. 2 mm long.

Differential Diagnosis

This is the largest flowered species of *Schizochilus* with sepal length varying from 4–11 mm. From the closely related *S. flexuosus* it can be separated by the yellow sepals, and usually by the lax inflorescence. From all other species it can be distinguished by the spur 4–6 mm long, and by the very acute, narrowly ovate lip lobes.

FIG. 17.
S. zeyheri Sond. *Linder 1996* from Graskop (Haenertsburg form), *Linder 2004* from Belfast (Lydenburg form)

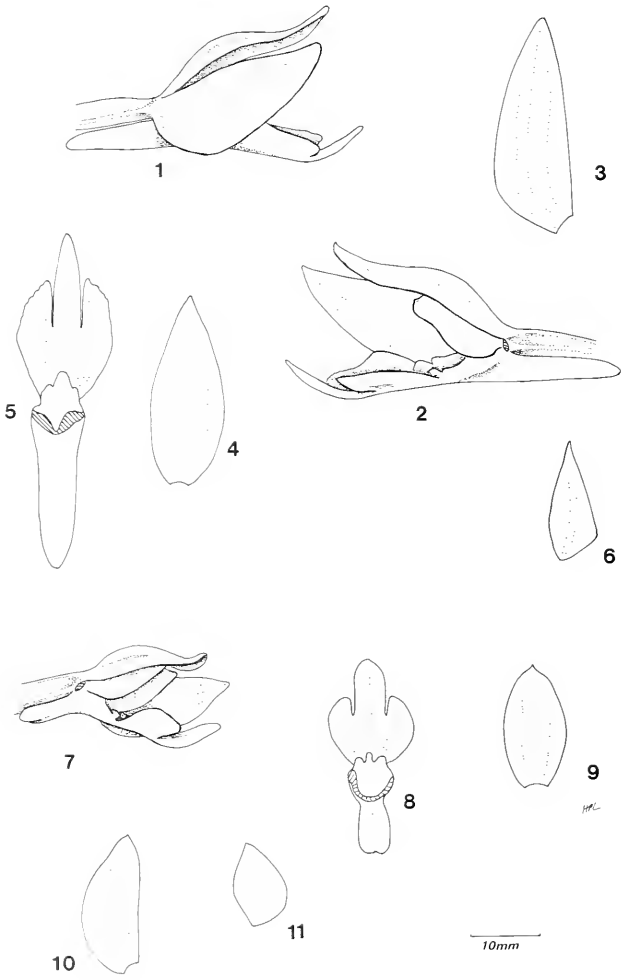

FIG. 18.
S. zeyheri Sond. 1 to 6 from *Hall 1150* (Port St. Johns, Pondoland Coast Form). 7 to 11 from *Linder 832* (Kaapsche Hoop, 2530 DB, Lydenburg Form). 1. Flower side view. 2. Flower side view with lateral sepal removed. 3. Lateral sepal. 4. Dorsal sepal. 5. Lip. 6. Petal. 7. Flower side view, lateral sepal removed. 8. Lip. 9. Dorsal sepal. 10. Lateral sepal. 11. Petal.

VARIATION

As can be seen from the description, this species displays a wide range of variation, most of which displays geographical patterns. Characters that vary are plant size, distribution of leaves, inflorescence shape, flower size and spur length. This variation forms the basis of the numerous species that have been segregated from this group by Rolfe (1912) and Schlechter (1921). The large amount of material collected over the last 50 years (the author studied 102 individual collections) reveals the patterns of variation clearly. Personal field studies have shown the range of variation found within single populations.

The variation among the geographical forms is summarised in Figure 19. Although the noda are distinct, they are linked both by extreme forms within populations, as well as by intermediate populations. This appears to be a case of partial geographic differentiation. *S. lepidus* Summerh. also forms part of this group, it is discussed below. The geographical forms in South Africa have not been given formal status, as too many intermediate forms exist. The published names are matched with the forms. However, within one population individuals can frequently be found that would segregate into different forms. The geographical forms are mapped tentatively; see Figure 20. The geographical forms are as follows:

(a) Haenertsburg form. Plants 400–600 mm tall, leaves scattered on scape, very narrowly lanceolate, flowers medium-sized, lateral sepals 5,5–7 mm long, spur 4–4,5 mm long.
   S. rehmannii Rolfe

(b) Lydenburg form. Plants small, 100–400 mm tall, leaves narrowly linear, mostly in a basal cluster, flowers small, lateral sepals 4–6 long, spur short, 3–4 mm long.
   S. strictus Rolfe
   S. clavatus Schltr.

(c) Natal form. Plants variable in size, from 200–600 mm, leaves narrowly lanceolate, scattered on the scape, flowers medium-sized, lateral sepal 4–9 mm long, spur 4–6 mm long.
   S. huttonae Schltr.
   S. bolusii Schltr.
   S. rudatisii Schltr.
   S. trilobus Rolfe.
   S. woodii Schltr.

(d) Pondoland Coast form: Plants generally large, 400–800 mm tall, leaves lanceolate, scattered on the scape, flowers large, lateral sepals 7–11 mm long, spur 5–6 mm long.
   S. sandersonii Rolfe
   S. grandiflorus Schltr.
   S. grandiflorus Schltr. var. *crenulatus* Schltr.

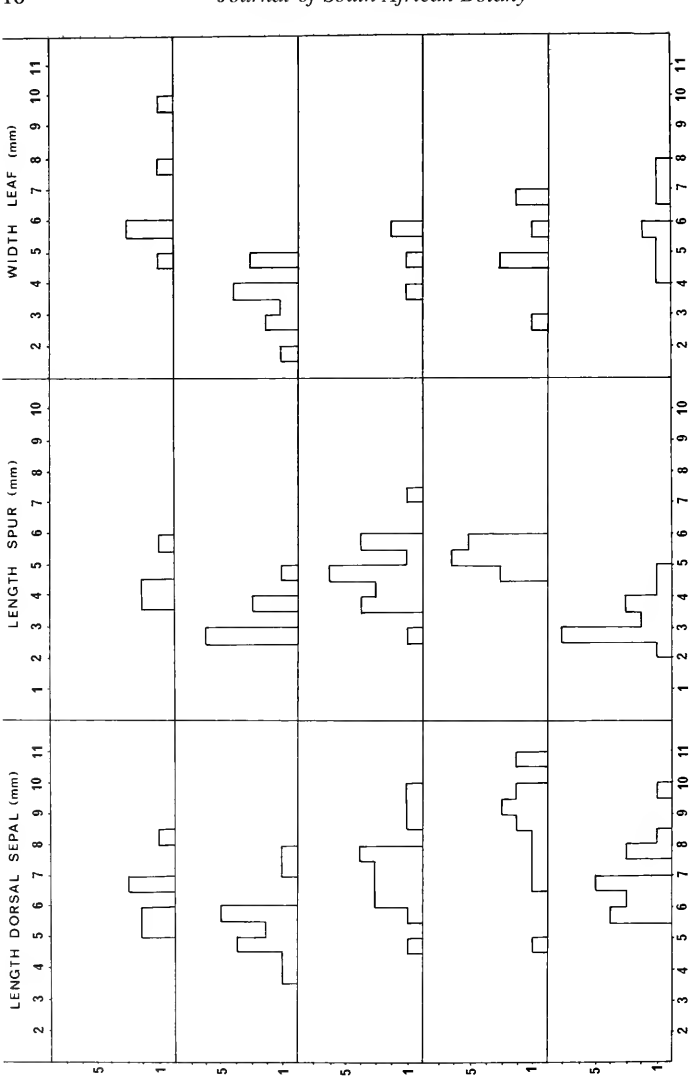

FIG. 19.
Variation in flower size (Dorsal sepal length), spur length and leaf width within and between the various forms of *S. zeyheri* described.

(e) Eastern Cape form: Plants 100–300 mm tall, leaves lanceolate, in a basal cluster, inflorescence subcapitate, flowers medium-sized, lateral sepals 6–8 mm long, spur 2,5–4 mm long.
S. zeyheri Sond.
S. caffrus Schltr.

There appear to be some general tendencies in the variation: populations from more tropical areas have larger flowers (long spurs, longer lateral sepals), and taller plants. Basal leaves appeared to have evolved twice in the colder areas (E. Cape mountains, Belfast-Lydenburg area). They are not sympatric with the basal leaved *S. flexuosus* Rolfe.

Nomenclatural Notes

S. zeyheri was the first species described in the genus *Schizochilus*, and serves as the type of the genus. In 1912 Rolfe published 4 names, and in 1921 Schlechter described 8 names, that have been reduced to synonymy. Rolfe's species, on the material then available, must have seemed reasonable species—there is one in each geographical form. However, the same cannot be said of Schlechter's concepts. He did not allow for any variation in spur length, flower size, or tepal shape. I do not propose to treat Schlechter's work in detail—he generally lists the reasons for separating taxa.

I have not seen any type material of *S. rudatisii* Schltr. and *S. clavatus* Schltr. These taxa have been placed into synonymy here on the basis of the protologues, and the recorded type localities. Of *S. grandiflorus* Schltr. I have only seen material of var. *crenulatus* Schltr.—this leaves little doubt that var. *grandiflorus* could also be included in *S. zeyheri* Sond.

Of *S. rehmannii* Rolfe I have only seen a collection of Atherstone, which was unlabelled, but agreed with Rolfe's protologue. The material clearly falls into the present concept of *S. zeyheri* Sond., but doubt must remain as to whether these collections are syntypes of *S. rehmannii*.

Biology

S. zeyheri occurs in Acock's (1975) Veld types 1, 8, 57, 44a and b. Of these the last four are different types of sour grassveld. (North-eastern Mountain Sourveld, Highland Sourveld and Dohne Sourveld and North-eastern Sandy Highveld), and only the Pondoland and Natal Coastal forms occur in coastal forest and thornveld. Over the whole distribution range, rainfall varies from 800 mm p.a. (Belfast) to over 1 500 mm p.a. (Eastern Transvaal Escarpment edge). In altitude the species ranges from near sea level, to 2 000 m, *S. zeyheri* can thus tolerate a wide range of variation in the macro-environment.

Over the most of this distribution range it occurs in swampy localities, often associated with Cyperaceae. Populations studied in Acock's Veld type 1 occurred

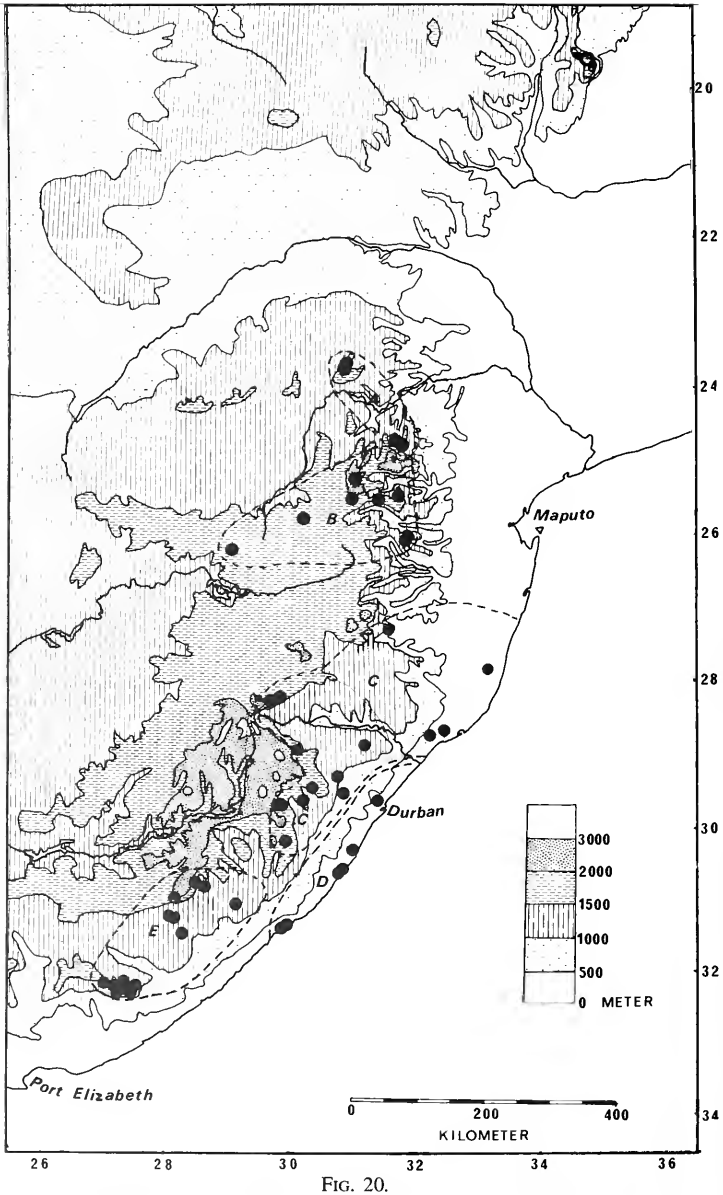

FIG. 20.
Distribution of *S. lepidus* Summerh. (○) and *S. zeyheri* Sond. (●)

in edaphic grasslands or swampy sites [*Linder 799*, Umgoye (2831 DC); *Linder 823, Port St. Johns (3129 DA)*]. Populations studied in sour grassland occurred mostly in secondary grassland, in seepages or swamps [i.e. *Linder 2004*, Belfast (2530 CA), *Linder 1996*, Graskop (2430 DD)], or in edaphic grassland in "dambos,' [*Linder 782*, Magoebaskloof Hotel (2330 CC)]. However, in the Eastern Cape this species occurs mostly on damp to wet rock ledges, often facing the coast in the mist belt zone. At Maclear it occurs in sour grassland [*Linder 2104*, Macler (3128 BA)]. In the Hogsback and Katberg Mountains, and King William's Town, *S. zeyheri* also grows on rock ledges, often in depauperate macchia. Story (1951) records frequent snow and frost in winter, and only 60% of the rainfall in the summer for this area.

The habitats of *S. zeyheri* in Natal and Eastern Transvaal are compared with other species from those areas in Figures 2 and 3.

This species appears to be common throughout its distribution range. Populations generally range from 30 to several hundred individuals. In swampy habitats the degree of sociability is low, but on rock ledges it is high. The flowers are pleasantly sweet-scented, and nectar has been detected in the spur. Nothing is known about the pollination biology. Flowering occurs from December to February.

Representative Material

Umkwani, Pondoland, X.1885, *Tyson 2605* (SAM!, GRA!, PRE!); Thomas River, King William's Town I.1893, *Flanagan 1689* (SAM!, GRA!, PRE!); Elandsberg, Stockenstrom, II.1886, *Scully* in *MacOwan & Bolus 3178* (SAM!, GRA!); between Belfast and Dullstoorn, 6.I.1979, *Linder 2004* (BOL!, PRE!, K!); Forbes Reef, Mbabane, 19.I.62, *Compton 31258* (NBG!, PRE!); Magoebaskloof Hotel, Haenertsburg, Pietersburg, 13.XII.1976, *Linder 782* (BOL!).

7. Schizochilus lepidus Summerh. in Kew Bull. **14**: 130 (1960): Type: Mozambique, Mt. Tsetsera, *Wild 4471* (K!, holotype; SRGH!, PRE!).

Plants slender, rarely subflexuose, 150–250 mm tall; tubers testicular, 10–20 mm long, ca. 5 mm in diameter; basal sheaths 2, white to hyaline, obtuse, apiculate, up to 30 mm long; leaves 8–12, scattered on the scape; the lower 2 to 5 narrowly oblanceolate to narrowly elliptical, 30–80 mm long, semi-erect, acute; the remaining leaves more or less sheathing, lanceolate, acute, ca. 10 mm long. *Inflorescence* semi-dense, 20–80 mm long, 20–30 flowered; ovary 5–7 mm long; bracts as long as the ovary, narrowly ovate, acuminate; flowers ca. 5 mm in diameter, yellow. *Sepals* subequal, three-nerved, acute to apiculate, 4,5–6,5 mm long; dorsal sepal elliptical, concave; laterals somewhat longer than the dorsal sepal, oblique, lanceolate to narrowly ovate, shallowly concave. *Petals* one-nerved, obliquely ovate-rhomboid, acute, 2,5–4 mm long. *Lip* 4–6,5 mm long;

epichile three-lobed, lobes subacute, central lobe 1–2,5 mm long, lateral lobes ca. half as long; disc with three obscure calli; spur subclavate, 1,5–2 mm long. *Anther* ca. 1,5 mm long.

Differential Diagnosis

S. lepidus is very closely allied to *S. zeyheri*, and can be differentiated from it by the spur 1,5–2 mm long and subclavate.

Biology

This species is only known from the Chimanimani Mountains between Melsetter and Vumba, in Zimbabwe. In this area it occurs above 2 000 m, in grassland (*Phipps 680*) or in rocky ground (*Wild 4471*). Rainfall in the area is approximately 1 400 mm p.a., of which most falls in summer (Jackson, 1961).

No scent has been recorded. Flowering occurs from January to March.

This taxon is clearly very closely related to *S. zeyheri*, from which it is isolated geographically. Morphologically, there is only a single character difference. According to the "rule of thumb" proposed by Hedberg (1958), this should be formally treated at subspecific level. This usage has been followed by Rourke (1972) and Tölken (1977). However, if this taxon were to be treated as a subspecies of *S. zeyheri*, the South African material would have to be treated as ssp. *zeyheri* [Article 26 of the I.C.B.N. (1978)]. But this material shows an enormous range of variation, which could almost be regarded as five subspecies. Hall (1969) dealt with the same problem, and suggested that the logical conclusion would be the naming of a single subspecific taxon. With present usage, however, the only alternative is to treat the Chimanimani material at specific level.

Representative Collections

Chimanimani Range, Melsetter, near Martins Falls, 6.II.1958, *Hall 377* (BOL!, SRGH!); Himalaya Range, Zimbabwe, 22.I.1955, *Ball 478* (SRGH!).

18. **Schizochilus sulphureus** Schltr. in Bot. Jahrb. **53**: 486 (1915): Type: Mt. Rungwe, *Stolz 1075* (B†, holotype; K!); Schltr. in Beih. Bot. Centralblatt **38**: 90 (1921); Summerh. in Fl. Trop. E. Afr. **156**: 27 (1968); Williamson, Orchids S. Central Afr.: 35, 213 (1977).

Plants slender, subflexuose, 80–200–(300) mm tall; tubers testicular, 10–20 mm long, ca. 7,5 mm in diameter; basal sheaths usually 2, the outer hyaline, obtuse, the inner white, obtuse to acute, up to 20 mm long; leaves 6–14, scattered on the scape, generally 2–5 clustered basally, semi-erect to deflexed, narrowly lanceolate to linear, acute, 20–50 mm long, the upper leaves grading into the floral bracts. *Inflorescence* semi-dense, 20–60 mm long, 15–40 flowered; ovary ca. 5

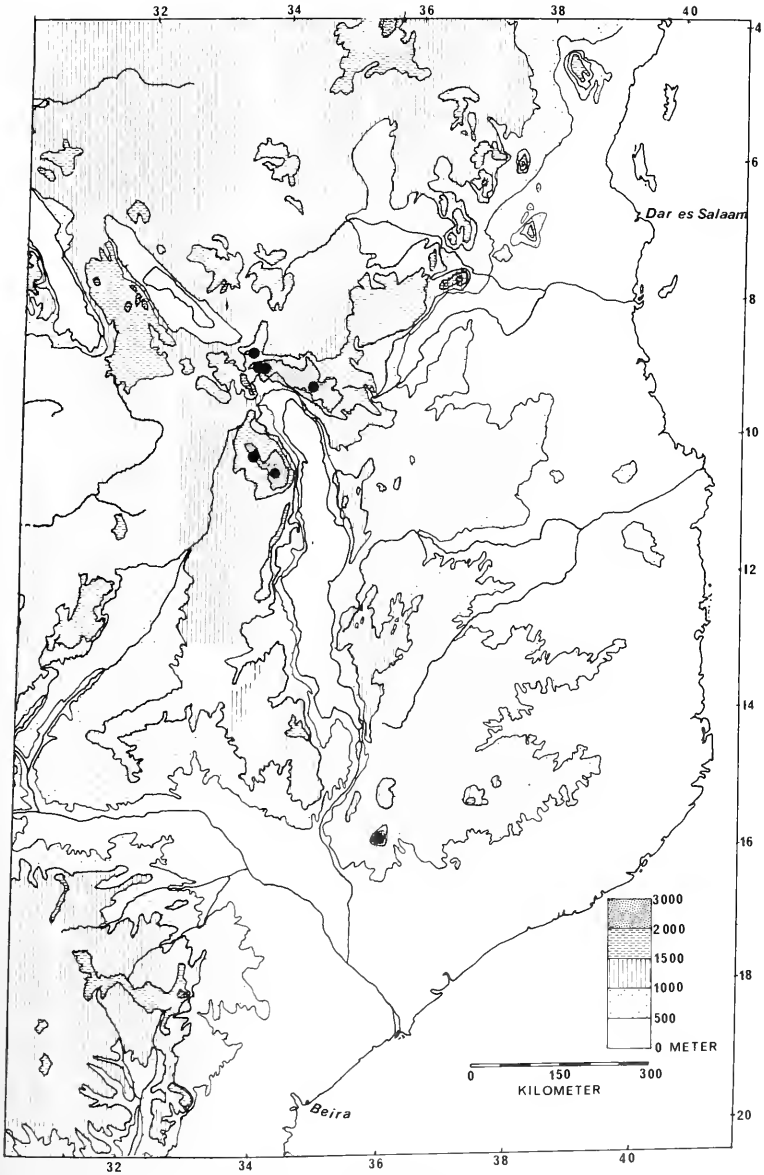

FIG. 21.
Distribution of *S. sulphureus* Schltr.

mm long; bracts slightly longer than ovary, narrowly ovate, acuminate; flowers ca. 4 mm in diameter, butter yellow, the petals somewhat paler than the sepals. *Sepals* subequal, three-nerved; dorsal sepal shallowly concave, elliptical to narrowly elliptical, obtuse to apiculate, 4,5–5,5 mm long; lateral sepals shallowly boat-shaped, suboblique, lanceolate, acute, 4,5–6,5 mm long. *Petals* single-nerved, oblique, rhombic-lanceolate, acute, 3–4 mm long. *Lip* 3,5–5,5 mm long, 1,5–2,5 mm wide; epichile three-lobed, central lobe subacute, ca. 1,5 mm long, lateral lobes obtuse, subobsolete, disc with three small calli; spur 0,8–1,2 mm long, curved towards the ovary. *Anther* ca. 1,5 mm long.

Differential Diagnosis

S. sulphureus is differentiated from the *S. zeyheri* group by the subobsolete lip lobes. The spur is shorter than 1,5 mm. The curved spur separates it from all other species of *Schizochilus*. It is the only species of *Schizochilus* that occurs north of the Zambezi.

Biology

This species occurs in the Afro-montane Zone (White, 1978) in the southern Rift Valley, between 1 800 and 2 500 m, mostly in secondary grassland. Recorded rainfall ranges from 1 750 mm to 2 000 mm on Mbeya (Kerfoot, 1964), 2 000–2 500 mm on Mt. Mulanje (Chapman, 1962), and from 1 000 to 2 500 mm on Nyika (Chapman and White, 1970). Snow does not occur, but mist and cloud are frequent. *S. sulphureus* is generally associated with rocky crevices or shallow soil over rocks. On Mt. Mbeya it occurs in the "Lithophytic Community" of Kerfoot (1964). Williamson (1977) records the habitat on Nyika Plateau as being "very wet montane grassland and wet peaty seepages on rock". On Mt. Mulanje this species was observed both in regularly burnt firebreaks, in mossy seepages over rock, as well as in moss on rocks in the proteoid scrub-land *(Linder 2005)*. The pollination biology of *S.sulphureus* is unknown. Scent has been recorded as being slight. Flowering occurs in January and February.

Representative Material

Malawi, Mt. Mulanje, Chilemba Peak, 12.II.1958, *Chapman 503* (K!, SRGH!, BOL!); Nyika Plateau, in rills, 10.II.1960, *Holmes 0203* (SRGH!, K!); Tanzania, Mbeya, rock clefts and crevices, 17.III.1960, *Kerfoot 1631* (K!).

9. **Schizochilus crenulatus** Linder, sp.nov.

Type: Graskop, Eastern Transvaal, 4.I.1979, *Linder 1995* (BOL, holotype; PRE, K).

S. zeyheri affinis inflorescentia laxa et sepalis 5–6 mm longis sed differt a calcaribus clavatis et callis filamentis, floribus albus nervatura malvinus differt, in saxonis humidus Transvaalensis orientalis crescit.

Plants very slender, sub-flexuose, 100–350 mm tall; tubers usually cylindrical, horizontal, two, rarely testicular; outer basal sheath very thin, hyaline, veins brown, apiculate; inner sheath white, apex green-tipped, acute, up to 40 mm long; leaves 5–6–(7); the lower 2–4 clustered basally, shallowly keeled, linear, acute, usually 70 but up to 100 mm long, ca. 4 mm wide; the remaining leaves scattered on the scape, grading from basal leaves into the floral bracts. *Inflorescence* a lax spike, nodding, 30–150 mm long, 6–25 flowered; ovary ca. 6 mm long; bracts half as long as the ovary, narrowly ovate, subacuminate; flowers about 5 mm in diameter, white with more or less mauve veins. *Sepals* subequal, three-veined; dorsal sepal galeate, narrowly oblong-ovate to oblong-ovate, apiculate, 5–7 mm long; lateral sepals shallowly keeled, suboblique, lanceolate to narrowly ovate, acute, often longer than the dorsal sepal, 5–7 mm long. *Petals* single-veined, subobliquely rhomboid, acute, curved over the anther and overlapping, 2,5–3 mm long and 1,5–2,5 mm wide. *Lip* 6 mm to 7 mm long, 3–4 mm wide; epichile three-lobed, the central lobe acute, ca. 2 mm long; the lateral lobes spreading or upcurved, rounded or truncate, usually crenulate, ca. 1 mm long; disc with a ridge of filamentous crests, hypochile relatively small, concave; spur straight, subclavate and bifid, 2–3 mm long. *Anther* erect, ca. 1,5 mm long.

Differential Diagnosis

This is the only species of *Schizochilus* with filamentous crests. It is readily distinguished from the other species with a lax inflorescence by the flower colour, and subclavate bifid spur.

Etymology

The name "crenulatus" refers to the crenulate margins of the lateral lip lobes, a characteristic which occurs only rarely in *S. zeyheri* Sond., and not in any other species of *Schizochilus*.

Variation

Although several populations were studied, very little variation was observed.

Biology

S. crenulatus is only known from the sloping plateau around Graskop. Acocks (1975) described the vegetation of this region as Veld type 8: North-eastern Mountain Sourveld. The grassland is described as being very sour, dominated by *Themeda triandra*, and as being derived from forests. Rainfall in the area ranges from 1 540 mm at Mac Mac, to 1 800 mm at Graskop (W.B. 29). Altitude in the area ranges from 1 500 to 1 800 m. In this area *S. crenulatus* occurs at the edges of flat Black Reef Quartzite rock flushes, in damp to wet conditions, and often in moss. The substrate is very rarely deeper than 10 mm, there is thus only

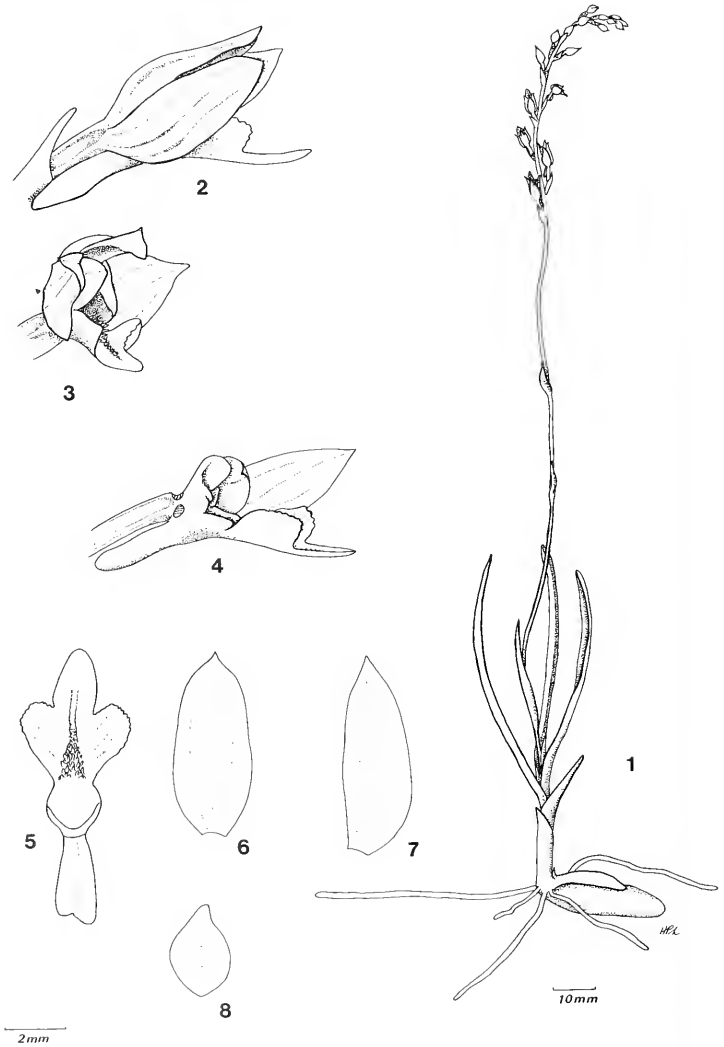

FIG. 22.
S. crenulatus Linder, from *Linder 1995* (type). 1. Whole plant. 2. Side view of flower. 3. Front view of flower. 4. Side view of column and lip. 5. Lip. 6. Dorsal sepal. 7. Lateral sepal. 8. Petal.

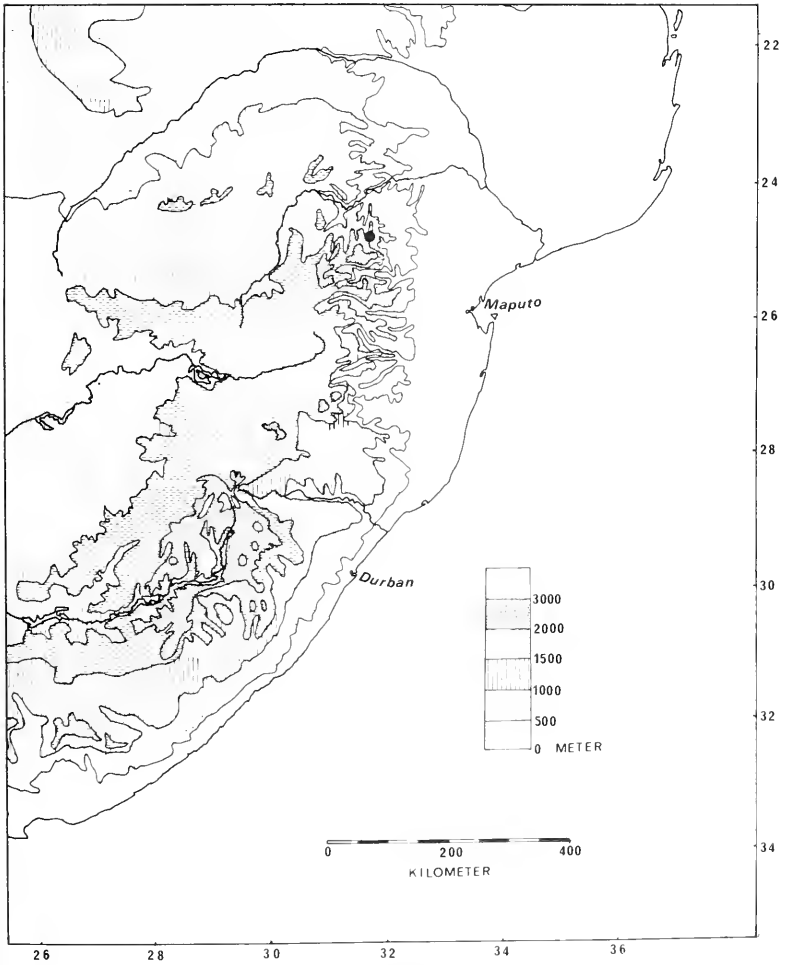

FIG. 23.
Distribution of *S. crenulatus* Linder

competition from mosses. The habitat is compared with that of other species of *Schizochilus* occurring in the area in Figure 3. Populations are large, ranging up to 200 plants. However, it is possible that there are very few populations, as these conditions only exist at the headwaters of streams. This species would have to be regarded as rare and vulnerable.

No scent or nectar could be detected, and regular seed-set occurred. The pollination biology is unknown. Flowering occurs from December to February.

NOMENCLATURE/HISTORY

This species was first collected by Galpin, probably in 1936. He sent living material to Mrs H. M. L. Bolus, in Cape Town, but it arrived in a bad condition, and Mrs Bolus thought that it might be a new species of *Cynorkis*. In February 1937 Galpin made another large collection, but the material was not studied. It is found in several herbaria under *Schizochilus indeterminavit*. In 1959 and 1961 Hall collected material, which was housed at BOL. Since 1975 several more collections have been made.

REPRESENTATIVE MATERIAL

Graskop, in moss on wet rocks, 4.II.1937, *Galpin 188* (BOL!, PRE!); Graskop, near Gods Window, on shallow rocks, 4.I.1979, *Linder 1998* (BOL!).

10. **Schizochilus lilacinus** Schelpe ex Linder, sp. nov.

Type: Graskop, Pilgrims Rest, in moist channel between two rocks, 2.XII.1937, *Galpin s.n.* (BOL!, holotype; PRE!).

Species insignis foliis 3–4 perangustis elliptibus, floribus albus nervatura roseus, callis filamentis; ab *S. zeyher* et *S. crenulato* sepalis lanceolatis 8–14 mm longis et petalis circa 3 mm longis differt; inter saxonis Transvaalensis orientalis crescit.

Plants slender, 200–350 mm tall; tubers testicular to cylindrical, up to 40 mm long; basal sheaths 2, the outer hyaline, obtuse, the inner white, acute, up to 40 mm long; leaves 3 or 4; the lower 2 or 3 near the base of the scape, semi-erect, shortly sheathing at the base, narrowly elliptical, acute, 40–100 mm long; the upper one or two leaves lanceolate, acuminate, erect, 20–40 mm long. *Inflorescence* semi-dense, up to 100 mm long, 3–25 flowered; ovary ca. 7 mm long; bracts somewhat longer than the ovary, narrowly lanceolate, acuminate; flowers ca. 10 mm in diameter, white or white with pink veins. *Sepals* subequal, three-nerved, lanceolate, acute, dorsal sepals 8–14 mm long, 2–3,5 mm wide; lateral sepals suboblique, 9–14 mm long, 2–3 mm wide. *Petals* single-veined, suboblique ovate, subacute, ca. 3 mm long. *Lip* 6–8 mm long, 2,5–3,5 mm wide;

FIG. 24.
S. lilacinus Schelpe ex Linder, from *Galpin s.n.* (type). 1. Whole plant. 2. Side view of flower with lateral sepal removed. 3. Side view showing column and lip. 4. Dorsal sepal, 5. Lateral sepal, 6. Lip. 7. Petal.

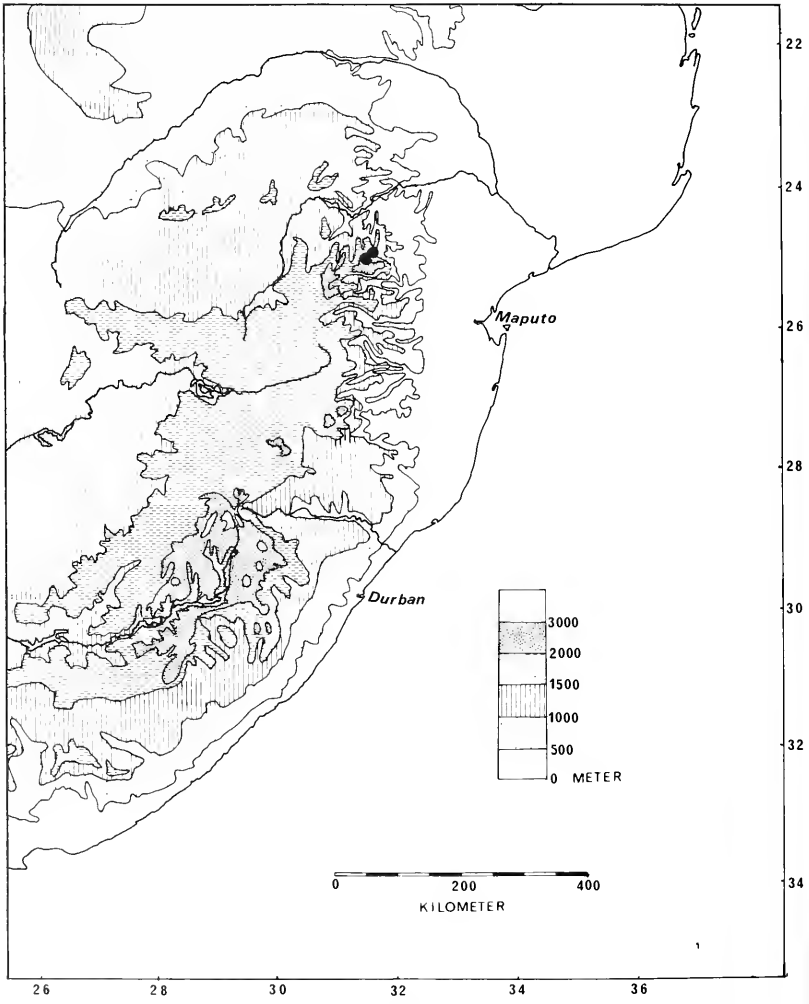

FIG. 25.
Distribution of *S. lilacinus* Schelpe ex Linder

epichile very obscurely three-lobed; central lobe 2,5–3,5 mm long, subacute; lateral lobes 0,2 mm long, upcurved; hypochile concave, ca. 2 mm long; disc with a small tuft of crests; spur deeply bifid, straight, 1,5–3 mm long. *Anther* ca. 2 mm long, straight.

Differential Diagnosis

This very distinct species can be recognised by the few large leaves, especially the 1–2 cauline sheaths; by the large flowers, by the petals only $^1/_3$ as long as the sepals, by the subobsolete lateral lip lobes and the bifid spur.

Biology

S. lilacinus has only been recorded from the Graskop-Lydenburg area, between 1 600 and 2 300 m above sea level. Acocks (1975) mapped the area as Veld type 8: North-eastern Mountain Sourveld. This is a secondary very sour *Themeda triandra* grassland. Rainfall at Graskop is about 1 600 mm p.a. (W.B. 29), There are no rainfall records for the summit of the Long Tom Pass. At the higher altitudes frost, and rarely snow, occurs.

In this general habitat, *S. lilacinus* occurs among rocks. A population studied on the Long Tom Pass was restricted to narrow ledges on a steep rocky slope, in soil ca. 40 mm deep, and occasionally in moss. The area could be described as damp.

No scent has been recorded, and the pollination biology is unknown. Flowering time is from October to December.

Nomenclature/History

Like *S. crenulatus* this species was first collected by Galpin in 1937, but no attention was paid to the new collection. Only in 1963 did Schelpe re-collect it, this time near the summit of the Long Tom Pass. Here it was re-collected in 1964 by Lavranos.

The specific epithet refers to the pale lilac colour that occasionally occurs in the flowers.

Representative Material

Summit Long Tom Pass, flowers white with longitudinal pink stripes, 2 100 m, 19.X.1963, *Schelpe s.n.* (BOL!).

Hybrids

The only hybrids reliably recorded are between *S. bulbinella* and *S. flexuosus*, from the summit of the Bushmansnek Pass, from Natal to Sehlabathebe in Lesotho (*Hilliard & Burtt 8928*). Both parental species were also recorded from the area (*Hilliard & Burtt 8926, 8927*). Field studies in the area revealed that the two

species were growing within metres of each other on a Cave Sandstone plateau, but the putative hybrids could not be recollected.

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INDEX OF NAMES IN THE REVISION

Names not recognised are printed in italics. Asterisks indicate figures.

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APPENDIX 1. LIST OF SPECIMENS STUDIED.

The specimens are listed alphabetically according to the name of the collector. The figures in brackets refer to the number of the taxon in the text. Herbaria from which each collection has been studied are indicated by the letter codes of Holmgren and Keuken (1974). Hybrid collections are indicated by combinations such as (5–7).

Acocks 10085 (6) PRE; *13963* (4) PRE; *21909*(7) PRE; *34579* (6) PRE—*Atherstone* (7) GRA, SAM.

Ball 358 (1) K, SRGH; *478* (8) SRGH; *498* (2a) SRGH; *795* (9) K; *952* (1) BOL, SRGH—*Balleine Payn 1* (7) GRA—*Barber 31* (7) GRA, K—*Batten* (7) NBG—*Bauer 630* (6) BOL, SAM; *631* (7) NBG—*Bayer 339* (6) NU—*Bayer & McClean 182* (5) PRE—*Bayliss 304* (7) PRE; *2541* (7) NBG—*Beasley 37* (2a) SRGH—*Beverley 441* (6) NU—*Bews 130* (7) NU—*Boardman 239* (3) PRE; *255* (6) PRE—*Bolus 12320* (2c) BOL; *12321* (7) BOL, PRE; (7) BOL—*Boughey 549* (2a) SRGH—*Broad* (6) NU—*Bromhead 58* (6) NU—*Bruce & Kies 70* (7) PRE, SRGH—*Bruyns-Haylett 37* (6) NU—*Buehrmann* (7) STE—*Bursell* in NU *7330* (5) NU—*Burtt Davy 1299* (7) BOL.

Campbell 1 (4) NU—*Chapman 503* (9) K, SRGH—*Chase 3601* (2a) SRGH; *4068* (2a) SRGH—*Codd 6729* (7) PRE; *8174* (2c) PRE, SRGH; *9733* (7) PRE—*Coleman 843* (7) PRE—*Collins* (7) PRE—*Compton 19194* (7) NBG; *24745* (7) NBG; *31258* (7) NBG, PRE—*Culver 76* (2c) BOL—*Cunliffe* (7) BOL.

Davies 859 (9) K—*Devenish 599* (7) PRE; *849* (7) PRE; *853* (6) PRE—*Dodd 8025* (7) PRE—*Doidge & Bottomley* (7) PRE—*Downing 278* (7) NU, PRE—*Dyer 374* (7) GRA.

Eastwood in PRE *14893* (7) PRE—*Ecklon & Zeyher* (7) S—*Edwards* (6) BOL.

Fannin 8 (7) TCD; *56* (6) TCD—*Fawkes 347* (3) NBG—*Fischer 1451* (2a) K, NU, PRE, SRGH—*Flanagan 1687* (7) GRA, PRE, SAM; *2671* (7) PRE; *2766* (7) PRE, SAM—*Fouché* (6) STE.

Galpin 188 (10) BOL, NBG, PRE; *713* (2c) GRA, PRE, SAM; *1144* (2c) GRA, PRE, SAM; *3416* (7) BOL, NBG, PRE; *6841* (7) GRA, PRE; *9569* (7) PRE; *10209* (7) PRE; *11727* (6) BOL, PRE, SAM; *13189* (7) BOL, PRE; *14438* (2b) BOL, PRE; *14450* (7) BOL, PRE; *14558* (11) PRE; in PRE *11768* (6) BOL, PRE; in PRE *14360* (2b) BOL, PRE; in PRE *14263* (7) BOL, K; (10) PRE; (11) BOL; (11) BOL, PRE—*Gerrard 1542* (4) TCD; *2176* (7) TCD—*Gerstner 2619* (7) BOL—*Gibson* (3) NU; *03* (6) NU—*Gilfillan* in Galpin *7251* (7) GRA—*Graham 50* (7) NU—*Grewcock* in PRE *27181* (7) PRE—*Grice* (6) NU—*Grosvenor 777* (2a) BOL, K—*Gunn* (7) PRE.

Hall 377 (8) BOL; *611* (7) BOL; *631* (2b) BOL; *632* (10) BOL; *819* (4) BOL; *864* (7) BOL; *865* (10) BOL; *963* (7) BOL; *966* (7) BOL; *1150* (7) BOL—*Harrison 82* (4) BOL—*Hart* (7) NU—*Haygarth* in STE *28* (7) STE; in Wood *9527* (5) GRA, NBG, SAM—*Henrici 1414* (7) PRE—*Hilliard 1135* (7) NU; *3049* (7) NU—*Hilliard & Burtt 3316* (4) NU; *4532* (9) K, NU; *6253* (9) NU; *7879* (6) NU, PRE; *7904* (7) NU; *8418* (4) NU; *8926* (6) NU; *8927* (3) NU; *8928* (3–6) BOL, NU; *9021* (6) NU—*Hoener 1791* (6) NU—*Hofmeyr* in PRE *31700* (7) PRE—*Holmes 0203* (9) K, SRGH—*Huntley 786* (7) NU—*Hutton 275* (7) GRA, PRE.

Jacobson 3814 (2a) K, PRE, SRGH—*Jacobsz 2523* (5) NBG, PRE— *Jacot Guillarmod, Getliffe & Mzamane 25* (6) PRE; *26* (3) PRE—*Jenkins* in PRE *6804* (7) PRE—*Johnstone 597* (7) NU.

Kerfoot 1631 (9) K—*Kerfoot, Gooyer & Eastman 31* (7) BOL; *33* (2b) BOL—*Killick 232* (7) NU; *1324* (6) PRE; *2299* (5) PRE—*Killick & Vahrmeijer 3588* (6) PRE; *4012* (6) PRE—*Kolbe 74* (7) GRA—*Kolbe & Pegler* (7) GRA.

Lavranos 3915 (11) BOL; *9348* (7) PRE; *9360* (2b) PRE; *15264* (2b) K, SRGH—*Leighton 2988* (7) BOL—*Lennon 80* (2a) K, SRGH; *81* (2a) K—*Linder 782* (7) BOL; *799* (7) BOL; *823* (7) BOL; *827* (7) BOL; *832* (7) BOL; *848* (7) BOL; *849* (2b) BOL; *850* (10) BOL; *937* (2b) BOL; *958* (6) BOL; *984* (3) BOL; *989* (6) BOL; *1007* (3) BOL; *1056* (7) BOL; *1071* (7) BOL; *1953* (4) BOL; *1960* (4) BOL; *1996* (7) BOL; *1997* (2b) BOL; *1998* (10) BOL; *1999* (2b) BOL; *2001* (11) BOL; *2002* (2b) BOL; *2004* (7) BOL; *2005* (9) BOL; *2049* (7) BOL; *2058* (7) BOL; *2077* (5) BOL; *2090* (3) BOL; *2091* (6) BOL; *2095* (3) BOL; *2104* (7) BOL.

MacOwan & Bolus 478 (3) BOL, GRA, SAM; *1378* (7) GRA, SAM—*Marais 300* (7) PRE; *318* (2b) PRE; *1454* (6) PRE—*McBean 74* (6) SRGH—*McClean 230* (6) PRE; *642* (6) PRE; *693* (6) PRE—*McKeown 74* (6) NU—*McLoughlin 36* (7) BOL; *115* (9) PRE; *179* (3) BOL; *196* (3) BOL; *302* (7) BOL; *403* (7) BOL; *428* (3) BOL; *486* (6) BOL, PRE; *501* (3) PRE; *532* (7) BOL, PRE; in PRE *13667* (3) PRE; (3) BOL; (6) BOL—

Meeuse 10062 (2b) PRE—*Mogg 13368* (7) PRE; *14671* (7) PRE; in PRE *31702* (2b) PRE—*Moll 627* (7) NU, PRE—*Murray 5* (7) PRE; *29* (7) GRA.

Newland 2 (10) PRE—*Nicholson 855* (7) PRE; *939* (7) PRE; *1357* (7) PRE—*Norlindh & Weimarck 4641* (2a) K; *4822* (2a) K; *4973* (2a) K.

Obermeyer 350 (2b) PRE—*O'Connor 288a* (7) NU; *315* (7) NU; *318* (6) NU; *335* (6) NU; *350* (7) NU; *355* (7) NU; *380* (7) NU.

Pegler 1431 (7) PRE; *1607* (7) PRE—*Phipps 680* (8) SRGH—*Pienaar* (7) NU—*Prosser1764* (7) PRE.

Rabie 2 (7) PRE—*Ratty* in Galpin *7320* (7) PRE—*Rennie 335* (6) NU; *517* (7) NU; *641* (7) NU; *730* (7) NU—*Reynolds 2661* (11) PRE—*Richards 7656* (9) K; *14250* (9) K; *14392* (9) K—*Richardson 37a* (2b) NU; *37* (7) NU—*Rogers 11533* (7) GRA, PRE—*Royffe 193* (7) GRA—*Rudatis 577* (3) STE; *2388* (7) STE—*Rutgers 7* (7) BOL.

Sanderson 564 (7) TCD—*Scheepers* in PRE *15022* (7) PRE; in PRE *31696* (7) PRE—*Schelpe 136* (5) NU; *137* (6) NU; *7199* (5) BOL; *7672* (5) BOL; *7692* (5) BOL; (11) BOL—*Schlechter 4028* (7) BOL, GRA, PRE; *6477* (6) BOL, GRA, PRE; *6482* (3) BOL, GRA, PRE; *6484* (6) BOL, GRA, PRE—*Schnitz 7014* (3) PRE—*Scully 1378* (6) BOL—*Shirley* (6) NU—*Sim 252* (7) NU; *957* (7) GRA, NU, PRE, SAM; *20064* (7) PRE; (7) BOL—*Simon 2323* (2a) K—*Smook 644* (6) NU—*Smuts 1063* (6) PRE—*Smuts & Gillett 2328* (2b) PRE; *2338* (2b) PRE; *2383* (7) PRE—*St. Clair Thompson 857* (9) K—*Stayner 104* (7) GRA—*Stephany 633* (6) BOL—*Stewart 1949* (5) NU—*Stolz 1075* (9) K—*Strey 7193* (7) BOL, NU, PRE; *9515* (7) PRE—*Sutherland* (6) K—*Symons 352* (6) PRE.

Taylor 263 (7) NU; *2045* (6) PRE—*Thode* in STE *3886* (7) STE; in STE *5745* (7) STE; in STE *8163* (7) STE—*Thompson* (7) NU—*Trauseld 367* (6) NU, PRE—*Tyson 1072* (3) BOL, GRA, SAM; *1600* (6) BOL, GRA, SAM; *2605* (7) GRA, PRE.

Van der Merwe 270 (2b) PRE; *281* (7) PRE; *1122* (6) PRE; *1535* (2c) PRE—*Van Jaarsveld 1025* (10) PRE—*Venter 5230* (7) PRE.

Wager in PRE *12499* (7) PRE; in PRE *31693* (7) PRE—*Walsh 28* (6) NU—*Ward 1120* (7) NU—*West 4636* (2a) K, SRGH—*Whellan 604* (2a) K, SRGH—*Wild 4471* (8) K, PRE, SRGH; *4939* (2a) SRGH—*Williamson, Simon & Ball 802* (9) K, SRGH—*Wilms 1397* (7) K—*Wood 478* (7) BOL; *3425* (7) BOL; *3444* (5) BOL; *3934* (6) BOL; *7735* (7) PRE; *9173* (7) NU; *9307* (7) NBG; *9527* (5) GRA, NBG, SAM; *10763* (5) PRE—*Wright 2174* (6) NU—*Wylie* in PRE *34251* (7) NU, PRE.

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THE VEGETATION OF THE EDITH STEPHENS CAPE FLATS FLORA RESERVE

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Abstract

The Braun-Blanquet approach was used to classify, describe and map the vegetation of the 3,5 ha Edith Stephens Cape Flats Flora Reserve. Vegetation patterns, species richness and life-form distribution are largely related to moisture conditions and thus to the slight variations in topography that occur in the reserve. The conservation value of the reserve is discussed.

Uittreksel

DIE PLANTEGROEI VAN DIE EDITH STEPHENS KAAPSEVLAKTE FLORARESERVAAT

Die Braun-Blanquet benadering is gebruik om die plantegroei van die 3,5 ha Edith Stephens Kaapsevlakte Florareservaat in te deel, te beskryf en te karteer. Plantegroei en lewensvorm verspreiding en soort-rykdom kan alles in verband gebring word met die beskikbaarheid van water wat weer verband hou met die effense variasies in die topografie van die reservaat. Die bewaringswaarde van die reservaat word bespreek.

Introduction

The Edith Stephens Cape Flats Flora Reserve, also known as Isoetes Vlei, is a 3,5 ha nature reserve falling under the jurisdiction of the Kirstenbosch National Botanic Gardens. The reserve is 14 km from the city centre of Cape Town, and is surrounded by land zoned for agriculture and by an urban area (Nyanga township).

The reserve was established in the late 1950s largely for the conservation of *Isoetes capensis*, a rare fern-ally that occurs in seasonal water-filled depressions on the Cape Flats. The present work was undertaken to provide an understanding of some aspects of the plant ecology of the reserve, to provide base-line data for assessing future vegetation change, to assess the conservation value of the reserve, and to determine management priorities.

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* This project was undertaken as an honours project by A. Gubb under the supervision of E. Moll. B. Campbell re-analysed the raw data and produced the present account.

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Methods

A feature of the study area is the marked vegetation seasonality. Field work for community classification and description by the Braun-Blanquet approach (cf. Werger, 1974) was undertaken from May to September, 1978. The vegetation was mapped in November with the aid of an aerial photograph taken at the end of the winter season (September). Sixty-one relevés of 4 m^2 were collected. All vascular plants and a single algal species, *Hydrodictum africanum*, were included in the study. The plant communities were recognised for mapping guided by a key that was constructed from the final phytosociological table (Table 1). Asterisks have been used to denote all introduced species.

Physiography and Climate

There is no more than 1 m of variation in topography in the reserve. The numerous shallow depressions are water-filled in winter but dry in summer. The waters in the reserve are probably alkaline (Stephens, 1929). Soils of the higher parts are sandy, whereas those of the low-lying areas are fine sandy loams to silt loams. The climate is Mediterranean—hot, dry summers and cool, wet winters. Mean annual precipitation is 534 mm. Only 10% of the rain falls in the four driest months (December to March).

The Plant Communities (Table 1)

1. **Lolium* community

   Structure: Tall (0,5 m–1 m) closed (over 50% cover) grass community; Dominant species: **Lolium multiflorum*; Differential species: **Medicago hispida*, **Rumex crispus*, **Vicia atropurpurea.*

2. *Ehrharta calycina-Pelargonium capitatum* community

   Structure: Mid-high (0,25 m–0,5 m) grass community with scattered shrubs; Differential species: *Ehrharta calycina, Pelargonium capitatum, Rumex ecklonianus, Rhus laevigata*, and *Pelargonium myrrhifolium* or *P. triste*; two sub-communities are recognised. The *Brunsvigia* sub-community (2.1) occupies a single hillock in the reserve. *Brunsvigia orientalis, Oxalis caprina, Satyrium odorum*, and *Lachenalia reflexa* were, amongst others, only recorded on this hillock. These species, **Bromus rigidus* and **Hypochoeris glabra* are differential species of the sub-community (2.2). The **Briza maxima* sub-community (2.2) is more extensive and occurs on slightly lower ground. A differential and dominant species is **Briza maxima*. Other differential species are **Lagurus ovatus, Arctotheca calendula* and **Avena barbata*. **Bromus molliformis* is a dominant in this sub-community and *Ehrharta calycina* is a co-dominant in both sub-communities.

3. *Felicia tenella* community

   Structure: Mid-high (0,25 m) grass and forb community; Dominant species: *Felicia tenella*; there are no differential species but this community is recognised by the lack of differential species of the more upland community (community 2) and also those of the more lowland communities (communities 4–6).

4. *Triglochin bulbosum* community

   Structure: Mid-high forb and low (0,1 m) grass community; Dominant species: *Trachyandra oligotrichum, Romulea tabularis*; Differential species: *Triglochin bulbosum, Sparaxis bulbifera*; this community is mainly differentiated from the following community by lack of *Aponogeton angustifolius*.

5. *Aponogeton-Sporobolus* community

   Structure: Variable—open to closed low (0,1 m) grass and forb community; Dominant species: *Sporobolus virginicus, Aponogeton angustifolius, Scirpus cernuus, Stenotaphrum secundatum* (none of these are constantly dominant); Differential species: *Diplachne fusca, Geissorrhiza juncea* (both have low constancy); this is an extremely variable community. It lacks good differential species but is distinguished from all the communities of more upland sites (communities 1–4) by the presence of *Aponogeton angustifolius.*

6. *Potamogeton-Aponogeton* vlei community

   Structure: Open hydrophyte community; Dominant species: *Potamogeton pusillus, Aponogeton angustifolius, Zostera capensis*; Differential species: *Potamogeton pusillus*.

The major environmental factor affecting vegetation pattern in the reserve is moisture. Slight differences in topography (0,05 m) affect moisture conditions. The vlei sites are generally not covered with more than 0,5 m of water in winter, have no surface water in late spring, and remain largely dry throughout summer. The upland sites (community 2), although not more than 1 m above the vlei sites, never have standing water. Communities 2 through to 6 occur on the gradient from upland to lowland (vlei) sites. Numerous transitions between communities occur. Transitional plots are included in the final phytosociological table. Community 1, the **Lolium* community, consists of introduced species which have invaded sites which might otherwise have been occupied by communities similar to communities 3 and 4 (*Felicia tenella* community and *Triglochin bulbosum* community). Thus the vegetation pattern shown in Figure 1 is largely related to slight changes in topography and to the extent of invasion of **Lolium multiflorum*.

There are very few published accounts of plant communities similar to those in the reserve. Stephens (1929) provides a general account of the fresh-water aquatic vegetation of the Cape Flats. She divides the seasonal vleis and pools into

TABLE 1.

PHYTOSOCIOLOGICAL TABLE OF THE PLANT COMMUNITIES OF EDITH STEPHENS NATURE RESERVE. Infrequent species have not been included in the table (list obtainable from authors). 0 = (+)

	1											2.1			2.2										3										4						5																		6		
Relevé number	1	61	59	17	55	60	58	56	54	53	57	50	51	52	39	44	43	47	40	45	46	49	42	48	35	36	41	19	38	37	29	34	30	33	32	27	28	26	25	31	24	18	20	21	16	15	14	11	13	22	12	10	2	9	8	3	5	23	7	6	4
Number of species	16	5	6	12	8	5	5	6	9	14	5	26	28	19	36	30	28	32	38	23	29	36	27	20	28	17	18	24	23	22	18	18	18	30	19	22	21	23	23	16	12	21	16	17	24	17	9	17	12	11	20	18	16	14	17	8	15	10	4	5	10
*Medicago hispida	0	+	+		2	2	+	1	1		2									0					0									+	0										0																
*Rumex crispus	2	2	2	2	0										+			0																										0	0	0			1			1	+							0	
*Vicia atropurpurea			+			2	2	0	0	0	0														0																																				
*Bromus ? rigidus					0			0				1	+	2	+							0																																							
Oxalis caprina												1	1	0																																															
Brunsvigia orientalis												0	0	2																																															
Carpobrotus edulis												3	0	0	2										0																																				
Babiana sp.												2	1					0																																											
*Hypochoeris glabra												2	1						0																																										
Lachenalia reflexa												+	+																																															
Satyrium odorum												+	0																																																
*Briza maxima															+	2	3	3	+	0	+	2	1	2																																					
*Lagurus ovatus															+	+	+	+		0		+	+	+			+							+																											
Arctotheca calendula															+	+	0	+	+		+			+																																					
*Avena barbata															+	+	+	+		2				1																																					
*Euphorbia peplus															1	0	+	+			0																																								
Wachendorfia paniculata															+	+	0		+					+																																					
*Bromus diandrus															+			0	2	2																																									
*Rumex angiocarpus															2	0			0					+				0																																	
Asparagus capensis																		0			1	1																																							
Ursinia anthemoides																				+	+	+	+	+										+											+																
Aspalathus niger																0	+	0																																											
Chasmanthe aethiopica																+	0																																												
Ehrharta calycina												1	3	1	2	2	0	+	+		+	+	1	0																																					
Pelargonium capitatum									0			1	0	3	1	1	0	+	+	+	0	+	+		0			+			+							0																							
Rumex ecklonianus												+	+	+	+	+	+	+	+	0	+	+	+		+	+										+	+																								
Rhus laevigata												0	0	0	1	1	0	1	1			2																					1	0																	
Pelargonium myrrhifolium/triste												2	0		2	1	2	+	+	1	1	3	2		2			+						+																											
Maytenus heterophylla												0	0	0	+		+																																												
Trachyandra ciliata													0	+							+	+																																							
Cotula turbinata													2					+				+												0											0																
Crassula glomerata																						+			+				+	+	1	+	+																												

Lachenalia glaucina		0 4		+ + +			
Monadenia micrantha			0 2 2	+ +			
Triglochin bulbosum							
Sparaxis bulbifera					2 + 1		
Crassula natans			+		+ 1 2	0 + 0 0 + +	+
Cynodon dactylon	2		1 1 1 2 0 1 1 0 2 0	2 1 1 + + 2 + + 0	0 2 +		
Scirpus antarcticus			0 + 1 + +	1 1 1 1 + + 1 1 1	+ + + 0 0	+	
*Briza minor			0 + + + + + + + +	+ 0 0 + 0 +	+ + +		
Cyperus tenellus			+ + + + 0	+ 2	+ + + + 2	2 2	
Cephalophyllum procumbens			+	2 + + 2	2 + 0 +	0	
Micranthus plantagineus				2 3 + + + +	+ + +		
Crassula decumbens				+ + 0 1 + 3	+ 1 +		
Diplachne fusca	0					0 2 3 0 3 3 2 0	0
Geissorrhiza juncea						1 2 2 2 2 + + +	
Isoetes capensis						2 1 4	
Cotula coronopifolia						0 + +	
Mariscus riparius						+ 3	0
Hydrodictum africanum						+ 2	3
Typha capensis						0 2	
Cyperus longus	1					2	
*Acacia saligna	0	+ + +	+ 0 + + + + + 0 +	0 + + 0 + 0 0 0 +	+ + 0 0 0	0 + 0 + + + 0	
Stenotaphrum secundatum	0	3	1 2 + 2 0	3 3 2 2 2	+ 0 + 0 +	0 1 + 3 + + 3 3 1 0 0 2 2 1	
Laurentia secunda	0	+ 0	0 + + + 0	+ + +	+ 0	0 0 + 0	
Cotula vulgaris		2	+ + 0 + 1	+ + + + +	+ 0	+	
Romulea rosea		1	+ + + 0	+ + 0	+ +	+ 0	
*Bromus molliformis	1 0		+ 1 2 + 2 2 2 2	+ 2 1 1 1 2 0 +	2 + + 0	+ 1 + 0 1 + 2 0	
Scirpus cernuus	0		+ + 0 + + + 0	1 1 1 1 1	0 + + 1 + 2	2 2 3 + + 1 2 + 2 + 2 +	
Micranthus junceus			1 + 0 + 0 +	+ + 1 0 0 1 1	1 0 + + 1	1 2 3 + + 2 0 0 + +	
Ficinia indica	0 +		1 2 + +	+ 1 2 2 + + 0	+ 1 0	+ 0 1 + + + 0 0 1 1 +	
Trachyandra ? oligotrichum	+ + 0		0 0	+ + 1 1 1 2 +	3 2 2 1 2 +	1 2 + 2 1 1 2 + 0 0 0 0	0 0
Hesperantha falcata			0 + 0 + 0 +	+	+	+ 0	
Schoenus nigricans				+ + 2 2 2 + 0	+ + 1 0 0	+ 2 1 + + + 0 0	
Romulea tabularis	+ 0	+	0 + + +	+ 0 2 2 1 1 +	2 2 2 2 2 1	+ 1 0 + + 1 1 + + 0 0 + 0 + 2	
Chrondropetalum tectorum				2	0	+ + 1	
Sporobolus virginicus	1			1 +	2 1 0 + 2 +	3 2 2 2 2 2 2 2 + + 1 1 1 2 1	0 0
Spiloxene aquatica					+ +	+ + + 2 0 + + 0 + 0 2 2	
Crassula expansa					0 +	0 0 + + + 3 0	
Potamogeton pusillus						+ 2	5 1 3
Aponogeton angustifolius			0			+ 1 2 0 1 3 1 + 2 + + 1 1 + 2 0 2 2	0 4 2
Zostera capensis						0 + 0 + 0 + 1 +	2 2
Zantedeschia aethiopica	0 0 0 0 0 + +	1 2 1	+ 0 + 0 + + 0 + 0	0 0 0 0 0 0	0 0 0 0	+ + 0 + 0 0 0 + + + 0	
Arthrocnemum capense				0 +	0 1 +	+ + 0 + + 0 0 + 2 +	2
*Sonchus oleraceus	+ 0 0			0		0	
*Vicia hirsuta	+		0			2	
*Anagallis arvensis		+ +			+ +		
Asparagus compactus		2	0				
*Lavatera sp.	0					2 +	
Juncus kraussi						3	

FIG. 1.
Vegetation map of the reserve. Sites of *Isoetes capensis* populations are shown by large dots.

marshes, lagoons, and open (i.e. not marshy) vleis and pools. Our *Potamogeton-Aponogeton* vlei community and much of our *Aponogeton-Sporobolus* community falls into her open vleis and pools category. Of our species she gives the following as characteristic: *Aponogeton angustifolius, Potamogeton angustifolius, Hydrodictum africanum, Isoetes capensis, Spiloxene aquatica*, and *Cotula coronopifolia*. All the other communities, apart from the most upland community (2), probably belong to Stephens' (1929) marsh category. She does not describe the marshes in any detail. Similar marsh communities are also recognised by Taylor (1972). He mentions such species as *Juncus kraussii, Chondropetalum tectorum, Cynodon dactylon* and *Stenotaphram secundatum*. Our upland community, the *Ehrharta calycina-Pelargonium capitatum* community, is undescribed elsewhere but is perhaps similar to Taylor's (1972) Inland Dwarf Fynbos, a type apparently found on mounds within the low-lying areas. The **Lolium* community, with its high complement of introduced species, cannot be related to communities described elsewhere.

Life Forms and Species Richness

The study area falls within Acocks' (1953) Coastal Macchia which is rich in phanerophytes (e.g. Acocks, 1933). In the reserve there is a relatively low percentage of phanerophytes and a predominance of the hemicryptophytic, geophytic and annual strategies (Table 2). This life-form spectrum is undoubtedly a result of (1) the very frequent fires in the reserve (the reserve has a wild fire almost every year—J. Marais, pers. comm.), and (2) the waterlogged conditions throughout summer and early spring.

Table 2.

Life form spectra (in percentages) of the species collected in the phytosociological survey. The life forms used are as follows: (1) P = phanerophytes: woody plants, > 250 mm; (2) C = chamaephytes: woody or sub-ligneous plants, < 250 mm; (3) H = hemicryptophytes: perennial herbaceous plants without underground storage organs; (4) G = geophytes: perennial herbaceous plants with underground storage organs; (5) T = therophytes: annuals.

	P	C	H	G	T	
Including introduced species	10	7	20	31	32	(136 species)
Excluding introduced species	12	9	28	43	8	(104 species)

The most lowland sites have a particularly short growing season for non-aquatic plants. In summer the soils are dry and hard, and in winter they are covered by water. Thus the few plants that do occur in the vleis are hydrophytes and hygrophytes (here classified mostly as hemicryptophytes, see Table 3). Species richness decreases from the upland plant communities to the lowland plant

communities (communities 2 through to 6; 29 species per relevé to 6 species per relevé). The decrease is in annuals, geophytes, and phanerophytes.

TABLE 3.
Species richness by life form in each community (average number of species per relevé, with percentages in brackets)

Community No.	1	2	3	4	5	6
Annuals (T)	4,7(57)	11,6(40)	9,2(43)	7,0(34)	3,2(22)	0,6(10)
Geophytes (G)	1,5(19)	7,8(27)	5,5(26)	5,6(27)	4,6(31)	1,4(22)
Hemicryptophytes (H)	1,4(16)	5,0(17)	4,8(22)	6,5(31)	5,5(38)	4,0(63)
Chamaephytes (C)	0,2(2)	0,7(2)	0,4(2)	0,5(2)	0,6(4)	0,3(5)
Phanerophytes (P)	0,5(6)	3,8(14)	1,6(7)	1,2(6)	0,7(5)	0 (0)
Total	8,3	28,9	21,5	20,8	14,6	6,3
Average % introduced species per plot	65	28	17	15	15	5

INTRODUCED PLANT SPECIES

Introduced plant species constitute a large proportion of the flora and the vegetation. About 20% of the species in the reserve are introduced.

The species of the **Lolium* community, including the dominant **Lolium multiflorum*, are mostly introduced annuals (Table 3). This community averages less than 4 indigenous species per relevé whereas the communities which it probably replaced average over 16 per relevé. This community covers about 25% of the reserve (Fig. 1). Apart from the *Potamogeton-Aponogeton* vlei community, all the other semi-natural plant communities (communities 2–5) have some **Lolium multiflorum* in them. One wonders whether these communities will also be converted to **Lolium* communities.

All the communities, except the *Potamogeton-Aponogeton* vlei community. have a high percentage of introduced species (Table 3). Apart from **Lolium multiflorum*, there are numerous other dominant or co-dominant introduced grass species in the reserve, especially in community 2. They are mostly European annuals (e.g. **Briza* spp., **Avena barbata* and **Lagurus ovatus*). Introduced herbaceous species are said to be confined to severely disturbed sites in the South-Western Cape (Kruger, 1977a). Disturbance in the reserve is in the form of fire; fires occurring almost every year (J. Marais, pers. comm.). Similar introduced annuals (**Avena* spp., **Briza maxima*) occur under completely different edaphic conditions on the much-burnt Signal Hill (Moll and Campbell, 1976). **Acacia saligna* forms dense shrub communities outside the reserve and, therefore, there are numerous seedlings inside the reserve. These are continually removed by the reserve managers.

Rare Plant Species

The only species in the reserve on the threatened plant list (Hall *et al.*, 1980) is *Restio sabulosus*. It is widespread in the South-Western Cape but occurs in very small populations (cf. Milewski, 1977). In the reserve the few clumps of this species are invaded by introduced grass species (**Lolium multiflorum*, **Briza maxima*).

Isoetes capensis, a rare fern-ally, was found at three sites in the reserve, all in the *Aponogeton-Sporobolus* community (see Fig. 1). *I. capensis* is found in rather temporary marshy sites in the south of the reserve. The sites were never covered with more than 150 mm of water, and generally lost their surface water rapidly. However, they remained damp for a few months as their soils have a relatively high silt component. Two of the three *Isoetes* sites appear to be in disturbed environments. One site is in the depression behind the man-made dune (made about 4 years ago) in the southeastern corner of the reserve, and the other is next to the firebreak and extends out of the reserve. This latter site appears to have been affected by the ploughing of the firebreak. The *Isoetes* population in the vlei in the northwestern corner of the reserve (E. Schelpe, pers. comm.) has apparently disappeared. Another major population used to be found on the site of the present double carriageway.

Conservation Value of the Reserve?

Is the conservation value of the reserve high enough to justify the expense of management? Will management be successful in, for example, controlling the spread of introduced grasses, and if not, should the money available for management be spent on other reserves or areas in which management will be more successful?

Questions like this indicate the need for an overall conservation policy for the South-Western Cape. At present we can only point out the conservation values of the reserve and the management policies that are necessary if the reserve is to be maintained in a worthwhile form.

The conservation value of the reserve is decreased by a number of factors:

(1) The small size (3,5 ha) and therefore the unlikelihood of the reserve being a viable ecosystem especially
   (a) as regards the lack of control of the quantity and quality of the much-needed water that enters the reserve, and secondly
   (b) the probable lack of long-term viability of many populations because of island effects. Kruger, 1977b, discusses minimum sizes of nature reserves;

(2) the dominance and spread of introduced plant species;

(3) the dense human population centre on the boundary of the reserve (Nyanga township) and therefore the disturbance of flora and fauna by the local inhabitants and their dogs;

(4) the very frequent fires and therefore the unnatural state of the plant communities.

If the reserve is to be conserved in a worthwhile state the managers will have to consider these problems.

The major value of the reserve is that it is the only area with natural seasonal open vleis and pools on the Cape Flats that is afforded conservation status. It also contains some rare species. The reserve has at least 126 indigenous plant species. Stephens (1929) suggests that the seasonal pools have a "rich amphibian, crustacean and other animal life". Preliminary check lists of plants, mammals, birds, reptiles and amphibians can be obtained from the authors, or from the Compton Herbarium, Kirstenbosch.

Acknowledgements

We would like to thank Mr B. McKenzie and Mr J. Marais for helpful discussions, and Jacqui Somerville for help with mapping of the reserve and with analysis of the data. We are extremely grateful to the staff of the Compton Herbarium for their generous help with the identification of plant material. Andy Gubb acknowledges financial assistance from the South African Council for Scientific and Industrial Research.

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CHROMOSOME ANALYSIS AND HETEROCHROMATIN RECOGNITION IN THE SOUTHERN AFRICAN SPECIES OF *ORNITHOGALUM*: 1. *ORNITHOGALUM SEINERI* (ENGL. & KR.) OBERM.

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Abstract

Ornithogalum seineri is an allohexaploid species with $2n = 6x = 24$. Its chromosome complement is bimodal with a basic number of $x = 4$, composed of three large (L) and one small (S) chromosomes. Quinacrine fluorescence staining shows a complex pattern of enhanced fluorescence bands only in the L-chromosomes.

Uittreksel

CHROMOSOOM ANALISE EN HETEROCHROMATIEN UITKENNING IN DIE SUIDELIKE AFRIKA SOORTE VAN *ORNITHOGALUM* 1. *ORNITHOGALUM SEINERI* (ENGL. & KR.) OBERM.

Ornithogalum seineri is 'n alloheksaploïede soort met $2n = 6x = 24$. Die chromosoom komplement is bimodaal met 'n basiese getal van $x = 4$, saamgestel uit die drie groot (L) en een klein (S) chromosome. Quinakriene fluoressensie toon 'n komplekse patroon van verhoogde fluoresserende bande slegs in die L-chromosome.

Introduction

The genus *Ornithogalum* in Southern Africa has been recently revised by Obermeyer (1978). It includes 54 species subdivided into three sub-genera. Only less than a third of the species have been examined cytologically.

In recent years the use of fluorochrome staining, and other advanced staining techniques for the linear differentiation of chromosomes, has revolutionised karyotype analysis and the understanding of chromosome structure (Vosa, 1975; 1977).

The present study, the first of a series, is concerned with the chromosome analysis and heterochromatin recognition of *Ornithogalum seineri* (Engl. & Kr.) Oberm., using the fluorochrome Quinacrine and Feulgen staining.

Material and Methods

The material consisted of plants collected in the wild by the present author in three localities in the Transvaal and subsequently cultivated in the cool greenhouses at the Botany School, Oxford. The localities of collection and the author's collecting numbers are indicated in Table 1.

For the cytological preparations generally, actively growing root-tips were pretreated in 0,05% colchicine in distilled water at room temperature for 3–4 hours, and then fixed in 1:3 acetic alcohol overnight.

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TABLE 1.
Collecting numbers and localities of collection of *Ornithogalum seineri*.

Collecting number	Localities of collection
1. *C. G. Vosa 445*	2331 (Phaloborwa): Phaloborwa (-AD).
2. *C. G. Vosa 1653*	2428 (Nylstroom): Potgietersrus (-AB).
3. *C. G. Vosa 1668*	2528 (Pretoria): Pienaarsrivier (-BB).

The Feulgen preparations were made according to the schedule suggested by Darlington and La Cour (1976) and the Quinacrine fluorescence preparations according to the schedule suggested by Vosa (1970; 1973).

RESULTS AND DISCUSSION

The Feulgen stained somatic chromosomes of *Ornithogalum seineri* are illustrated in Figure 1. The karyotype consists of 24 chromosomes and includes 18 large (L) and 6 rather small acrocentric chromosomes (S). The S-chromosomes are about one fourth of the L-chromosomes. Thus, the complement of *O. seineri* presents a striking bimodality, which is indeed found in many species of the subgenus *Urophyllon* (Vosa, in prep.).

There are up to six L-chromosomes with a nucleolar attachment distally located in the short arm, but only two are usually visible in most metaphases (Fig. 1).

FIG. 1.
The Feulgen stained somatic chromosomes of *Ornithogalum seineri*. The arrows indicate the two most prominent nucleolar constrictions (× 2500).

Figure 2 shows the chromosome complement, stained with Quinacrine and Figure 3 its diagrammatic representation.

Quinacrine staining shows at once a complex pattern of enhanced fluorescence bands (Q-bands) in all L-chromosomes and, on the basis of such patterns and size, they can be subdivided into three groups of six chromosomes. The S-chromosomes do not show any banding but, on the basis of their morphology, they can be subdivided also into three groups.

The repetitive band patterns of the L-chromosomes and the overall morphology of the S-chromosomes indicate that *O. seineri* is hexaploid with a basic number of $x = 4$ (3L + 1S).

It is known that Quinacrine fluorescence is enhanced by the presence of repetitive sequences of Adenine-Thymidine (AT) nucleotides and that Guanine-Cytidine (GC) nucleotides effectively quench its fluorescence, even when they are regularly intercalated in an otherwise AT-rich sequence (Weisblum, 1973; Weisblum and de Haseth, 1972 and see Vosa, 1975 for discussion). The results show that the repetitive DNA sequences, which represent the heterochromatic segments of *O. seineri*, are composed, probably almost exclusively, of AT-nucleotides.

FIG. 2.
The Quinacrine stained chromosomes of *Ornithogalum seineri*. Note the despiralised procentric segments of most of the chromosomes (arrows), × 2500.

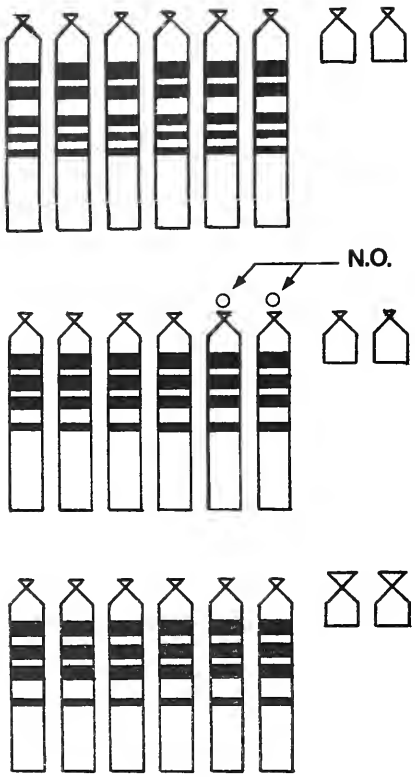

FIG. 3.
The diagrammatic representation of the Quinacrine stained karyotype of *Ornithogalum seineri*. Note the most prominent nucleolar chromosomes (N.O.).

It is interesting to note that, besides producing discrete fluorescent patterns, Quinacrine staining seems to despiralise, or otherwise stretch, the chromosome segments between the centromere and the first band in all L-chromosomes (Fig. 2, arrows). The mechanism of such an occurrence is not known at present but it resembles the *in vivo* despiralising effect of the fluorochrome Hoechst 33258 on the heterochromatic segments of some mammalian chromosomes (Hilwig and Gropp, 1973). In the case of *O. seineri*, however, the despiralisation occurs in fixed chromosomes and in non-heterochromatic segments.

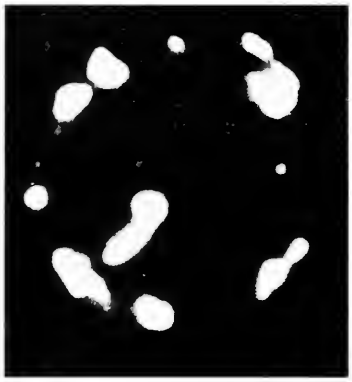

FIG. 4.
Interphase nucleus of *Ornithogalum seineri*. Note the fluorescent chromocentres (× 2500).

The interphase nuclei of *O. seineri* present prominent chromocentres which vary in number with a minimum of about 4–5 (Fig. 4). In middle prophase nuclei, the despiralised euchromatic segments can be seen attached to four or more highly fluorescent chromocentres (Fig. 5).

The three collections examined are very similar to one another both cytologically and morphologically.

O. seineri is a widely distributed species (Obermeyer, l.c.). In all three localities of collection the species occurs in drifts of up to one hundred plants, mostly of flowering size but with a fair number of smaller plants and seedlings, showing a high degree of fertility.

Preliminary observations of meiotic stages have shown regular bivalent formation and pollen fertility seems to be about 75-80%.

The results show that *O. seineri* is an old established allopolyploid species, well adapted to dry conditions and found, typically, in overgrazed sandy flats, where it is probably protected by its alleged poisonous properties.

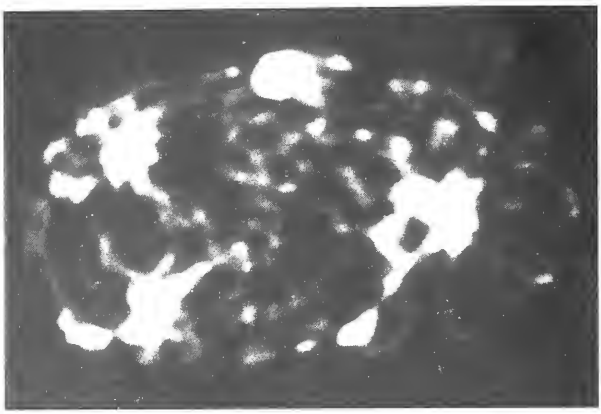

FIG. 5.
Middle prophasic nucleus of *Ornithogalum seineri*. The euchromatic chromosome segments are attached to the chromocentres (× 2500).

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Book Reviews

Plant Cell and Tissue Culture: Principles and Applications, edited by W. R. Sharp, P. O. Larsen, E. F. Paddock and V. Raghavan. Columbus, Ohio: Ohio State University Press. ISBN 0-8142-0287-X. List price US $37.50

This book, the title of which differs only by transposition from that edited by the late H. E. Street (*Botanical Monographs*, Vol. II, 1973), is dedicated to the memory of this pioneer in the area of *in vitro* culture, and is based on a colloquium held at the Ohio State University in 1977. It is unfortunate that it took the editors two years to publish the proceedings since much of the information to hand at the time was novel and some of the ideas far-reaching.

The 37 contributions have been organized into four parts: (1) global status of food and agriculture, (2) physiology of growth and morphogenesis, (3) genetics and (4) agricultural applications. Of the 10 papers in the first part only two actually deal with *in vitro* culture; the others, one assumes, were probably intended to indicate the kinds of problems (food production) to which future TC research might be directed. Parts 2 and 3 contain little that has not been said before, and it is perhaps to be expected that with international TC symposia of one kind or another occurring with such regular frequency, that stalwarts such as Steward, Cocking, Gamborg, Butenko, and others will find it increasingly difficult to report "breakthroughs" on each occasion.

Part 4 is, in my opinion, the heart of this book since most of the 17 papers deal with issues of practical consequence, that is, the application of *in vitro* culture methods to agriculture, horticulture and forestry. Sommer's and Brown's contribution on the application of tissue culture to forest tree improvement is well-researched and their reference list is extensive and thorough. Tsai-Ying Cheng who, as one of the most imaginative and enthusiastic of workers has been a leader in the area of mass clonal micro-propagation for the last five or more years, gives a good account of the current status of *in vitro* techniques as they apply to *Pseudotsuga menziesii* (Douglas fir), a tree of great economic importance in the U.S.A. and fast becoming so in parts of Europe, for example, France.

In this regard one misses a contribution by M. Boulay of AFOCEL (France) who, perhaps more successfully than anyone else, has gone a long way in bridging the gap between the *in vitro* regeneration of some of the conifers and their commercial outplanting.

The book contains nearly 1 000 pages, is studded with specialist information and pertinent references and, on balance, is good value for money.

Chris H. Bornman

In Vitro Culture of Higher Plants: Bibliography, by R. L. M. Pierik, with pp. 149. Distributed by Kniphorst Scientific Bookshop, Box 67, 6700 AB Wageningen, Netherlands. December, 1979. US $27.00

Were it not for the indication "Bibliography" in small print on the attractively illustrated cover page, the title of this book could be misleading. Under the title *In Vitro Culture of Higher Plants* the author has mainly collected a list of surnames (in many cases only those of senior authors) and abbreviated journal citations pertaining to applied aspects (vegetative propagation) of plant tissue culture. About 70% of the volume of the book is made up of entries such as, for example: Arora en Singh. 1978. Curr. Sci. 47: 867–868. Similarly, genera and species from which haploids or from the embryos of which whole plants have been regenerated are also listed. Orchids merit a separate section of the book, as does mericulture in relation to freeing clonal material of pathogens. A section titled "Test-tube fertilization" has 21 entries, while the author rounds off his book by indulging briefly in some journal-listings statistics.

The information in the book is no doubt based on R. L. M. Pierik's own extensive offprint collection and as such is incomplete, although his own work is fully cited. To have any real value the entries should carry full citations and be organised more specifically in accordance with the many branches of the subject. Otherwise it cannot—and I sincerely trust it does not—replace the bibliography section of the *IAPTC* (International Association for Plant Tissue Culture) *Newsletter*, as the author in his rather naïve preface hopes it might. (The bibliography listed in the quarterly *IAPTC Newsletter* covers aspects of physiology, biochemistry, genetics, secondary products and cytodifferentiation and is reasonably up-to-date. References are fully cited and, in addition, the country in which the research was undertaken is also indicated.)

Pierik's book provides limited source material and at the price of US $27.00 is also too expensive. One cannot avoid the feeling that a large part of the price is intended to defray the cost of the 18 colour pictures on the cover.

CHRIS H. BORNMAN

PROCEEDINGS OF THE THIRD NATIONAL WEEDS CONFERENCE OF SOUTH AFRICA, 1979, with pp. 214, 85 figures and tables. Obtainable from the publisher: A. A. Balkema, P.O. Box 3117, Cape Town. Hard cover R20,80.

These proceedings, edited by S. Neser and A. L. P. Cairns on behalf of the Southern African Weed Science Society, have appeared two and a half years after the proceedings of the Second National Weeds Conference. Like their predecessors these proceedings set out to be nothing more than a record of the papers presented on a variety of weed subjects but, in lieu of other readily available published material on weeds in the sub-continent, they will be elevated almost automatically to the status of a "national review" and will be prescribed reading for anyone interested in our weed problems.

Twenty-six of the forty-two papers read at the conference are reproduced in this volume. They include two highly topical reviews. The first provides a fascinating picture of the stages in the development of herbicides "from synthesis to reality", including the many hazards, the precautions that have to be taken and the considerable financial risks involved. It will be an eye-opener both to those who wonder why more and better herbicides are not more readily available, and to those who decry their use.

A second paper of note is that by a visitor from Zimbabwe on the role that minimum-tillage has to play in reducing agronomic weed problems, in conserving the energy (both chemical and mechanical) put into weed control, and in conserving the whole farming environment.

The chemical control papers are mainly concerned with the control of weeds in our staple cereal crops, and they deal in some detail with the respective merits of pre- and post-emergence application of herbicides, and the determination of the best growth stage of the crop for post-emergent applications.

Other chemical control aspects dealt with are: factors influencing the use of atrazine in maize (the most important single herbicide/crop relationship in South Africa at present) and the aerial application of herbicides to encroaching woody species (an important pasture and sensitive environmental problem).

There is encouraging news, from a representative of the Department of Forestry, on progress with the mechanical eradication of *Hakea* and there are several papers on forestry weeds and their control in general. Biological control is represented by descriptions of possible control agents for *Acacia longifolia* (Sydney golden wattle) and *Sesbania punicea*.

Other papers include reports on: woody plant invaders in the central Transvaal, Austrialian *Acacia* species in the S.W. Cape, Nassella tussock infestation on Devil's Peak, *Aristida junciformis* (ngongoni), *Cyperus rotundus* (red nutgrass), *Opuntia ficus-indica* (prickly pear), and *Myriophyllum* (water milfoil or parrot's feather).

In the preface mention is also made of other important developments in weed control in

South Africa, e.g. the success story of the control of *Eichhornia crassipes* on Hartebeespoort Dam, and the provision of a National Weed List.

These proceedings cover a period when there has been strongly burgeoning interest in weeds and a growing realization of their impact on both production and conservation. They provide an invaluable record of the development of the science as well as providing information on particular problems and their solutions.

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INDEX OF PLANT NAMES

Note: Plant names appearing in tables or lists are not included in this index. Page references to new taxa are printed in bold type. An asterisk indicates an illustration.